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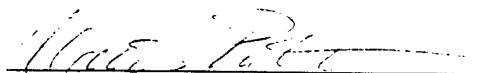| 17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT

THESIS ABSTRACT

This study represents an analysis of regeneration processes for eastern white pine (*Pinus strobus* L.). The objective is to develop an integrated approach to evaluate the influence of factors that, alone and in combination, determine regeneration outcomes.

This study is composed of three sections. The first chapter is a literature review of white pine regeneration dynamics. The purpose is to present a process for understanding the regeneration process of a single species and present a conceptual approach to integrated evaluation of influential variables. Six interrelated ecological factors (seed tree density, competition, disturbance, seedbed conditions, soils, and damage agents) were identified and their impact on the regeneration process is evaluated. A conceptual model of the integration approach and two examples of how this approach can be utilized in assessing regeneration operations are presented.

The second chapter is an analysis of the growth response of planted white pine seedlings to varying levels of competition. Overstory cover was manipulated by harvesting to establish a range of crown closures. Competition from understory vegetation was studied through annual or monthly removal of competing vegetation and investigating the response of the seedlings. Overstory density along with the competitive influence of understory woody vegetation were found to be important to both height and diameter growth. Damage from herbivory was the greatest impediment to survival of seedlings on this site. White pine blister rust and white pine adelgid seems to be more prevalent in open grown seedlings.

The third chapter describes the development and testing of a process based model for evaluating the interactions of influential factors on the recruitment, early growth, and survival of white pine germinants. The purpose is to generate a multifactoral response surface to test decision choices and their potential implications. Sensitivity and model application tests are conducted to evaluate conditions under which factors are important and the efficacy of management activities. Recruitment, early growth, and survival are sensitive to seed and safe site availability, stand composition and structure, and a range of mortality factors.

_____ Dr. Klaus J. Puettmann, faculty advisor

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Dr. Klaus J. Puettmann, faculty advisor

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June 12, 2002
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GRADUATE SCHOOL

The Assessment and Modeling of Regeneration Dynamics for Eastern White Pine (*Pinus strobus* L.)

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
By

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
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CHAPTER 1

An integrative review of the regeneration ecology of

eastern white pine (Pinus strobus L.)

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An integrative review of the regeneration ecology of eastern white pine (Pinus strobus L.)

Abstract

A broad multifactor approach was used to examine key ecological processes that impact the natural regeneration dynamics of eastern white pine. Published and ongoing field studies were reviewed to identify how various factors and processes influence eastern white pine (Pinus strobus L.) regeneration and how an integrated examination regeneration may limit risk and improve the capacity for land managers to optimize management strategies. Six major biotic and abiotic elements are discussed: disturbance, soils, seed production and distribution, seedbed conditions, competition and biological damage agents. These factors are then reviewed to establish their influence on regeneration and under which conditions these factors (singly or in combination) steer the regeneration process towards cohorts (i.e., even-aged groups) or towards recurring establishment of single trees (i.e., uneven-aged groups). Management decisions that may alter these factors and thus influence white pine regeneration outcomes are described. The clearcut and shelterwood systems are used to illustrate the integration of these factors for management purposes.

Keywords: eastern white pine, regeneration dynamics

Introduction

Forest regeneration dynamics are driven by inherently complex factors and interactions. Despite this complexity, single factors are often selected for the purpose of prescribing silvicultural treatments related to regeneration (e.g., shade tolerance in Table 1, Silvicultural Interpretations Working Group 1994 pg. 13). Selection of single factors is, at least partially, based on the importance of these factors and on the availability of information. Recent reviews have pointed out that a single factor analysis may not be sufficient to adequately explain the regeneration ecology of a tree species (e.g., Greene et al. 1999). Moreover, in some cases it may even be misleading to attribute a regeneration outcome to the influence of a single variable (Messier et al. 1999a). I propose an alternative, more integrated view of the regeneration process that focuses on the interaction among various factors that influence the regeneration process. For this, I conducted a detailed examination of ecological processes that drive regeneration patterns for eastern white pine (Pinus strobus L.).

My review of the regeneration process suggests that white pine regeneration is primarily a function the following six factors:

(i)   In sites that rely on natural regeneration the density and vigor of overstory white pine provides an indication of seedfall availability and dispersal potential.

(i)   Interspecific and intraspecific competition: a function of composition and density of the overstory, shade tolerant mid-story species and understory vegetation layer.

(ii)   Disturbance regime: provides information on site-specific opportunities for regeneration.

(iv)   Seedbed conditions after seedfall.

(v)   Soil type/characteristics.

(vi)   Damage potential from insect, disease and animals.

Each of these six factors represents a gradient of conditions and which combine to form an interrelated matrix where factors potentially affect each other factor (Figure 1.1).

The potential range of regeneration success, which results from these interactions, is considered a continuum from no seedlings (or failure of regeneration) to single tree recruitment to the establishment of even-aged cohorts.

Conditions at a specific time on a specific site are characterized by a unique amalgamation of these factors. The resulting regeneration dynamics are not simply driven by linear links, but include dynamic and non-linear feedback loops and interactions. While I obviously cannot discuss all possible modes of interactions, I provide an examination of each factor, using published literature about eastern white pine.

My intent in the development and presentation of this examination of the regeneration process is twofold. First, I want to point out that there are unique characteristics or qualities possessed by white pine related to the regeneration process. The second and more important goal is to organize knowledge of these characteristics for integration into a generic process oriented regeneration model. This paper represents the first step in identifying and assessing interactions and processes that impact regeneration success. To illustrate the usefulness of this technique, I examine the integration of these factors using two common silvicultural prescriptions for white pine: clearcut and the shelterwood system.

Background

The silvics of white pine have been explored for well over 100 years; for a detailed overview on the silvicultural characteristics of the species see Pinchot and Graves (1896), Spalding and Fernow (1899), Frothingham (1914), Horton and Bedell (1960), Horton and Brown (1960), Wilson and McQuilkin (1963), Lancaster and Leak (1978), Stiell (1978), Lancaster (1984), Stiell (1985), Stearns (1992), Chapeskie et al. (1989), Day and Carter (1990), Wendel and Smith (1990), and Kershaw (1993).

White pine has a broad ecological amplitude demonstrated by its vast native range, extending from the western Lake States to eastern maritime Canada and south along the Appalachians to northern Georgia (Richardson 1998). It grows on a variety of soils and is classified as intermediate shade tolerant (Shirley 1943, Baker 1949, Wendel and Smith 1990). This physiological adaptation to shade and associated climate and

resource conditions allows white pine to regenerate under a wide range of conditions (Abrams 2001). It can behave like a typical pioneer species by invading old-fields or following a major disturbance. On the other extreme, white pine can behave as a mid-to late-successional species by invading the understory of existing forest stands that have not recently experienced major disturbances (Wendel and Smith 1990).

Traditionally, white pine regeneration has been linked to large-scale disturbances. Maissurow (1935), after surveying white pine stands in Quebec, formed the hypothesis that fire was necessary for white pine to become a component of forest canopies. Maissurow's hypothesis motivated much of the research on white pine regeneration for almost 50 years. In contrast, Hibbs (1982), Carleton et al. (1996), and Abrams (2001) describe the mid- to late-successional behavior of the species and hypothesized that white pine might successfully recruit to the canopy of uneven-aged forests in the absence of fire. Quinby (1991) indicated that, although large-scale surface fires encouraged white pine seedling establishment, white pine self-replacement was frequently driven by the creation of small canopy gaps.

Six factors driving regeneration patterns

Seed availability and dispersal

For natural regeneration, the vigor and density of overstory white pine is a critical factor and can act as a metric for the potential availability of seed. Abundant seed allows the recruitment of expansive cohorts of white pine seedlings. Conversely, limited seed availability, even when coupled with favorable site conditions may yield only individual recruits or isolated pockets of regeneration.

Potential seed production of white pine is related to the density of seed trees. In stands with a low white pine density, the canopy position, vigor of the tree, local site topography, and wind patterns impact seed production and dispersal and thus influence regeneration (Ahlgren 1976, Rudis et al. 1978, Greene and Johnson 1989). Timing of seed production is crucial. If seed production is low when site conditions are favorable for recruitment, regeneration of non-target species may result (Kershaw 1993, Schupp 1995, Dovčiak et al. 2001). Conversely, if site conditions are unfavorable (e.g., after

establishment of non-target species), low germination rates or poor establishment and growing conditions will prevent white pine seedling establishment.

Good white pine seed years occur on average every 3 to 5 years with bumper crops typically every 10-13 years (Wendel and Smith 1990). White pine can begin to bear cones in 15-20 years, but maximum seed production occurs between 50 and 150 years of age (Lancaster and Leak 1978, Stiell 1978). Seed production is driven by individual tree vigor, e.g., dominant trees may produce twice the number of cones of co-dominants (Wendel and Smith 1990).

White pine cones require two years from formation until ripening, and a number of factors (e.g., weather patterns, insects) may reduce or eliminate seed production during this interval (Wendel and Smith 1990). Thus, until late summer of the second year, i.e., around 2 to 3 months prior to seed dispersal, a good cone crop does not guarantee high seed availability. Average germanitive capacity of seed at dispersal is between 65-90% (Stiell 1978, Krugman and Jenkinson 1989). White pine does not "seed bank" and germination of seeds in the second year following dispersal is uncommon (Krugman and Jenkinson 1989, Kershaw 1993).

Research on white pine seed production as a function of overstory conditions is limited to a single study in Maine USA (Graber 1970). In that study, viable seedfall peaked in medium density (around 30 m2/ha basal area (BA)) white pine stands at 4.4 million seeds/ha in a good seed year and 1 million seeds/ha in a poor seed year. Under low-density conditions (around 20 m2/ha BA) seedfall was 3.1 million seeds/ha in a good seed year and 736,000 seeds/ha in a poor seed year (Graber 1970). Higher density stands (around 40 m2/ha BA) yielded diminished seed production to 2.8 million seeds/ha in a good seed year and 736,000 seeds/ha in a poor year. This pattern is likely due to the limited number of seed trees at low density and diminished vigor due to dense stocking at higher density (Stiell 1978).

Following seed production, seed dispersal has a significant impact on the recruitment process. Dispersal within a stand and to adjacent areas depends on several factors and numerous models have been proposed to describe this process and analysis conducted to determine influential factors (e.g., Geritz et al. 1984, Greene and Johnson 1989, Ribbens et al. 1994, Houle 1995). Important attributes include canopy structure,

composition, topography, extent of the stand, size of the recruitment site and proximity to the seed source (Peterson and Carson 1996, Cornett et al. 1997). The tall stature of mature trees, combined with the high wing length/seed weight ratio favors wide spatial dispersal of the seeds (Richardson 1998). Winged seeds have dispersal patterns that generally follow an inverse decay curve (Okubo and Levin 1989). Specific dispersal patterns are a function of the combination of the height of the seed tree, wind direction and speed, and shape and weight of the seed (Okubo and Levin 1989). In one study, seed rain density necessary to fully stock (>5,000 seedlings/ha) a clearcut strip adjacent to a residual stand only occurred within 20 m of the residual stand boundary (Hocker 1968). Even with the assistance of favorable prevailing winds, seedfall decreased to negligible amounts within 40 to 80 m from the boundary. However, within a white pine/aspen (Populus tremuloides Michx.) stand, Palik and Pregitzer (1994) observed that areas further than about 100-140 m from seed trees had few white pine seedlings and delayed recruitment when compared to areas near seed trees. Maximum horizontal dispersal potential for seed from canopy trees is considered to be 60 m within a stand and over 200 m in the open (Wendel and Smith 1990).

Importance of competitive conditions

Interspecific and intraspecific competition is considered one of the primary mechanisms of interaction among plants (Oliver and Larson 1996). Such interactions influence regeneration by altering resource availability. For example soil water, nutrient availability and ambient light quality and quantity at both the micro-topographic scale and landscape level. Site factors like soil, air temperature, and wind patterns contribute to the interaction dynamics (Caldwell et al. 1995). Successful recruitment is a function of competitive and related influences that are altered by the site-specific vegetative composition and structure. Characterizing stand structure, here described by the various plant layers, helps determine the degree to which white pine seedlings must compete for scarce resources or grow in sub-optimal environmental conditions. Site or stand level characterizations of the stand structure provide a tool to help foresters predict the extent of the potential white pine regeneration. Although resource utilization varies by species, we have an understanding of the negative impact of resource competition on white pine

seedlings (Schugart et al. 1992, Elliot and Vose 1994, Oliver and Larson 1996, Burgess and Wetzel 2000). Often, white pine is associated with 'nutrient poor-well drained' sites (Leak et al. 1995). For a review of the morphological and physiological adaptation of conifer seedlings to different growing conditions, see Wetzel and Burgess (1994), Boucher et al. (1998) and Counte (2000).

The most evident reaction of seedlings to competition is a reduced growth rate. In northern Minnesota, height growth in white pine saplings is reduced by competition from overstory trees, but is less sensitive to competition from understory vegetation (Saunders and Puettmann 1999a). The influence of competition is reflected in the growth response of white pine when suppressed trees are released. Suppressed white pines, like most species, typically respond with accelerated diameter and height growth after release is accomplished (Geerinck et al. 1954, Stiell et al. 1994, Puettmann and Saunders 2000). The negative relationship between competition and growth patterns is a keystone of silvicultural operations aimed at allocating cumulative growth increment.

The release-growth response is not limited to juvenile saplings. White pine older than 50 years have shown the physiological capacity to respond to release as have trees suppressed for a long time (up to 4 decades) (Brace 1978, Kelty and Entcheva 1993). Puettmann and Saunders (2000) report that the magnitude of the release-growth response varied with individual tree conditions and pre-release tree height growth. The response of trees growing slowly before release was quicker and more intense, while the growth response of trees that were growing quickly before release was not as great. Also, the intensity of release (partial vs. complete removal of the overstory) was related to the magnitude of the growth response (Puettmann and Saunders 2000).

In multistoried stands, the competitive component most influential to seedling growth is often site specific and varies based on disturbance history, site fertility, and stand development phase. The manipulation of any vegetation layer with the intent to alter competition is feasible, but it is important to consider the integrated response of all vegetation layers.

Overstory influences

The overstory represents an important component of a stand's competitive influence and thus the overstory density and composition provide a measure for predicting the potential success or failure of white pine regeneration processes. Other conditions being equal, decreasing overstory density will increase resource availability and permit increased biomass accumulation in seedlings (Berry 1982, Brand 1990, Canham et al. 1996, Smidt and Puettmann 1998, Saunders and Puettmann 1999a).

One major influence of the overstory on growing conditions of seedlings is its effect on the quantity and quality of light transmitted to the forest floor (Atkins 1957, Federer and Tanner 1966, Counte 2000). Under conditions where there are multiple resource limitations, light reaching the forest floor influences regeneration and establishment of seedlings by its effect on carbon allocation and moisture and temperature conditions (Canham et al. 1996, Pinno et al. 2001). Increasing overstory density decreases both the quality and quantity of light available for seedlings. A minimum light intensity of 20% of full sunlight is desirable to ensure seedling survival (Logan 1959, Lancaster and Leak 1978). Several studies (Shirley 1945, Logan 1962, Gatherum et al. 1963, Logan 1966) revealed that white pine can achieve maximum height growth in 40 to 55% of full light conditions. On the other hand, diameter growth continues to increase with light availability to 100% (Logan 1959). This capacity to survive and grow under partial shade conditions has been utilized in the practice of regenerating white pine using a two or three cut shelterwood system (Heeney 1978, Lancaster and Leak 1978, Wendel et al. 1983, Wray 1986, Day and Carter 1990, Kelty and Entcheva 1993, Burgess et al. 2000).

Various authors have recommended retention of a partial residual overstory or understory component as a means of controlling understory competition (Wendel et al. 1983, Lieffers et al. 1993, Smidt and Puettmann 1998). Smidt and Puettmann (1998) suggested that managers focus white pine regeneration efforts in areas that had relatively dense overstory basal conditions prior to a shelterwood cut. When a proportion of the overstory is retained there appears to be benefits which include reduced seedling mortality and better growth due to the pre-existing suppression of competing vegetation.

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Burgess and Wetzel (2000) report improved nutrient uptake and optimal white pine seedling growth when the 100+-year-old coniferous overstory was thinned to a two-crown spacing. Harvest activities reduce competitive conditions provide and opportunity for white pine seedlings to become established. Such a strategy may not succeed on mesic/fertile sites where the shade tolerant understory response may be vigorous (Carleton et al. 1996). Maintaining a residual overstory for 10 years after seedling establishment allows white pine to reach an age where it can grow at the same rate or better than most competing hardwoods (Kelty and Entcheva 1993).

Overstory species composition also influences recruitment, especially seedling emergence and mortality. A recent study determined that white pine had both a higher emergence rate and a higher mortality rate under a conifer canopy when compared to a deciduous canopy type (Cornett et al. 1998). The presence of aspen, a pioneer species that quickly becomes established in dense stands, in the overstory may inhibit pine recruitment (Peterson and Squiers 1995). In dense stands of juvenile aspen, light transmission to suppressed seedlings may be as low as 4% of above canopy light levels, creating severe light limitations in the understory (Pinno et al. 2001).

Midstory influences

The impact of a dense layer of shade tolerant midstory vegetation can have on the regeneration process can be significant. Midstory trees are usually shade tolerant species (throughout much of the range of white pine); such as sugar maple (Acer saccharum Marshall), red maple (Acer rubrum L.), and balsam fir (Abies balsamea (L.) Miller)). In stands with a dense midstory, light penetration to the forest floor can be reduced to such a low level that white pine recruitment is precluded and only the most shade tolerant species can survive (Shirley 1945).

In addition to attenuation of light resources, midstory tolerants compete for nutrients and moisture. This not only influences seedlings directly, but also indirectly through suppression of competing layers of understory vegetation. In one study, after removal of the midstory, chances of white pine recruitment were improved as competing understory vegetation was slow to recover (Puettmann and Smidt 1997). On productive

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sites, successive release operations may be necessary in instances where shade tolerant midstory species recover more rapidly than the white pine (Methven and Murray 1974).

Shrub layer influences

The development of dense shrub layers may occur throughout the range of white pine. In the Lake States region, heavy herbaceous and shrub competition is a major cause of regeneration failures (Buckman 1964, Brand 1990). Hazel (Corylus cornuta Marshall and Corylus americana Walter) competition is especially problematic in northern Minnesota and where these species grow in thick clumps, which over time expand horizontally via clonal development (Buckman 1964). In the Appalachians of the southeast US, rhododendron (Rhododendron maximum L.) and mountain laurel (Kalmia latifolia L.) are common understory competitors that also grow in thick clumps and have similar influences on pine recruitment (Balmer and Williston 1983, Neary et al. 1984). Weak disturbance patterns often result in shrub layers becoming denser (Neumann and Dickman 2001). The capacity for white pine seedlings to survive or maintain vigor under intense competition from a thick shrub layer is often limited to individuals whose microsite conditions favor the pine over competitors.

Herbaceous layer influences

Evidence of the ability of white pine to recruit in the presence of herbaceous competition is apparent in extensive white pine cohorts in old-field successional patterns (Minckler 1946, Lutz and Cline 1947, Foster 1988, Gill and Marks 1991, Barnes et al. 1998). White pine succession in old-fields is often associated with even-aged cohorts in the northeast US. Old-fields were typically abandoned grass covered hay-fields or pasture in which white pine seeded from adjoining areas (Barnes et al. 1998). Disturbance created by agriculture or logging was the key factor in eliminating competing species favoring the recruitment of white pine (Lutz and Cline 1947).

However, where grass communities are well established and grow in tall dense patches the interspecific competitive influence can mimic those of an established overstory. Caldwell et al. (1995) reported that the presence of grasses limited light, altered growth rates, and changed micro-environmental factors for seedlings. For

example, at a seedling height of 20 cm, incident photosynthetically active radiation (PAR) was reduced to 30-55% and 75% of full light conditions in the first and second growing season, respectively. Several studies have shown that the presence of a dense, tall herb layer early in the establishment phase, especially grasses, can significantly reduce the recruitment and growth of juvenile pine (Caldwell et al. 1995, Wagner et al. 1996, Wagner et al. 1999).

Understory vegetation layer dynamics are typically viewed as an important component of the total competitive environment. The development of the herb layer is a direct result of the overall competitive conditions and structure of the stand (Maguire and Forman 1983). The annual composition and spatial arrangement of the herb layer varies in response to environmental conditions that are a function of the floristic mosaic of the site (Maguire and Forman 1983). Cornett et al. (1998) found white pine seedling mortality rates during the first year and over winter were lower in experimental plots where weeding removed herbaceous competition, perhaps because herbaceous plant removal through weeding increases moisture or soil nitrogen availability to seedlings (Thevathasan et al. 2000). The vertical development of trees typically conveys a competitive advantage over herbaceous plants in the long run, but the slow vertical development of white pine seedlings may allow intense competition from understory species to develop during the first few years (Lancaster and Leak 1978, Counte 2000).

Disturbance

The role of disturbance events

The one factor most often associated with white pine regeneration is disturbance (Abrams 2001). Large and small disturbances create windows of opportunity for recruitment to occur and potentially succeed. In essence, the specific characteristics of the disturbance may drive regeneration success. While species are often characterized by their ability to respond to disturbances, the specific response of individual trees and stands to disturbances varies with a variety of factors, including age and vigor. (Oliver and Larson 1996, Barnes et al. 1998). Disturbances have three defining characteristics related to regeneration dynamics of white pine: severity, spatial extent, and disturbance frequency, (Heinselman 1981, Vitousek and White 1981).

Disturbance mechanisms commonly associated with large cohorts of pine regeneration include fire; windthrow or human-based disturbance primarily associated with logging, weed control, or land use conversion, e.g., agricultural practices (Mirov 1967, Richardson 1998). It is interesting to note that although white pine is known to regenerate successfully following most types of disturbances, regeneration success following logging in the late 19th and early 20th centuries in the Lake States was generally poor (Cope 1932, Hough and Forbes 1943, Horton and Bedell 1960, Heinselman 1973, Oliver and Stephens 1977, Van Wagner and Methven 1978). This is likely due to a combination of the elimination of seed sources, frequent and intense fire cycles and the emergence of increased deer herds and subsequent herbivory (Abrams 2001).

Disturbance events alter both biotic and abiotic site factors and play various interrelated roles in the outcome of white pine recruitment. First, a disturbance of sufficient intensity and spatial extent creates openings in the overstory and/or midstory (Webb 1986, Oliver 1980). This increases light penetration to the forest floor and reduces nutrient and water uptake from competing vegetation, resulting in increased resource availability for seedlings. Openings in the forest canopy also result in increased surface soil temperatures and fluctuations in temperature and soil moisture (Childs and Flint 1987, Counte 2000). Second, disturbance events alter seedbed conditions, for example by exposing mineral soil. Exposure of mineral soil also results in increased temperatures on the forest floor, which affect the timing and success of seed germination (Smith 1951, Graber 1968, Fraser 1970, Heckman 1992). Third, disturbance events may eliminate or reduce disease and insect infestation vectors (Logan 1951, Smith et al. 1997).

Disturbance events alter numerous soil characteristics at various spatial and temporal scales. For example, soil compaction or changes in bulk density result from logging and intense fire events. Compaction resulting from mechanical operations such as logging can explain differential recruitment for all tree species across a site. Suckering species like aspen, which are one of the major competitors for white pine in the Lake States, appear sensitive to soil disturbance and/or compaction (Arikian 2001). Similarly, each disturbance event has a unique impact on nutrient cycling, site level fertility, and a

host of soil micro and macro fauna communities in forest soils (Burgess and Wetzel 2000, Marshall 2000).

Chapman (1947) suggested that disturbances were necessary for perpetuation of most forest types and that most of the old-growth white pine in the Lake States originated after fires. Following a disturbance of sufficient severity, e.g., a major fire, white pine has the ability to act as a pioneer species (Maissurow 1935, Ahlgren 1976). Maissurow (1935) noted that stand-changing fire resulted in large tracts of even-aged white pine forests in Quebec. Across much of the range the occurrence of pine is associated with past patterns of fire disturbance (Wood 1932, Spurr 1954, Horton and Bedell 1960, Heinselman 1973, Methven 1973, Ahlgren 1976, Stiell 1985, Whitney 1986, Day and Carter 1990, Tester 1995, Clark and Royall 1996).

Land use changes, specifically agriculture, represent a different type of disturbance event that results in the elimination of most or all native vegetation from a site for an extended period of time. This basically eliminates the local seed bank. After abandonment of farming the land is typically colonized through invasion from adjacent land. In New England, regeneration of even aged stands of white pine and white pine-northern hardwoods mix is common on abandoned farm fields (Lutz and Cline 1947 and 1956, Smith et al. 1997). White pine regeneration on old-fields has been recognized since the 1860's and used as a regeneration tool in the eastern US (Cope 1932, De Steven 1991, Smith et al. 1997).

Severity and spatial extent of disturbance

Severe catastrophic disturbances of large spatial extent remove most or all of the existing stands cover and precedes regeneration processes typically associated with an even-age class cohort (Maissurow 1935, Heinselman 1973, Abrams and Orwig 1996). Severity, as used in this study, refers to the impact a disturbance event has on the structure and or follow-on composition of a stand. Large-scale disturbances have profound impacts on the forest and successional pathways. For example, Heinselman (1973) reports that just five fire events occurring over a 70-year period from 1840-1910 in the Boundary Waters Canoe Area Wilderness (BWCAW), Minnesota ($\approx$ 400 000 ha) resulted in origination of 90% of white pine stands present today.

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Small-scale disturbances, even when severe, have vastly different impacts on successional processes (Oliver and Larson 1996). Small-scale disturbances typically remove a few trees in an isolated location. The ecology of gap-phase replacement associated with small-scale disturbances is a well-documented ecological process and I refer the readers to the following for further information (Shugart and West 1980, Shugart 1987, Canham 1989). Small-scale disturbances may create canopy gaps that allow for single-tree replacement by advanced regeneration or germinants (Runkle 1982). Juvenile white pine growing in the understory compensate or acclimate physiologically to light limitations through allocation of photosynthate to survival mechanisms (e.g., below ground biomass, crown morphology) which result in reduced above ground growth rates but facilitate survival in the understory (Pacala et al. 1994, Canham et al. 1996, Messier et al. 1999, Counte 2000, Puettmann and Saunders 2001). Acclimation allows the tree to remain suppressed for significant periods of time and potentially take advantage of canopy gaps as release mechanisms.

While even fairly small canopy gaps created by disturbances may afford isolated and suppressed white pine the opportunity to reach the overstory, gap-phase dynamics likely play a minor role in landscape level white pine recruitment and large-scale disturbances are more important (Hibbs 1982, Day and Carter 1990). Although gap-phase succession is typically associated with tolerant hardwoods in temperate forests, long-term continuous recruitment of white pine in response to non-catastrophic disturbance has been documented (Hibbs 1983, Holla and Knowles 1988, Quinby 1991, Abrams 2001). Abrams and Orwig (1996) described white pine as a gap-phase species in northwestern Pennsylvania. Single-tree recruitment may be more common on marginally productive sites. Ziegler (1995) concluded that white pine was self-replacing in gaps on sandstone outcrops in relict old growth stands in southwestern Wisconsin, US. Also, small-scale disturbances that affect only the mid- or understory have a beneficial effect on suppressed white pine. A goal of prescribed burning programs is an attempt to mimic small-scale disturbance patterns present prior to European settlement.

Catastrophic windthrow is a less frequent natural disturbance event in temperate forests (Foster and Boose 1992, Barnes et al. 1998, Palmer et al. 2000). Although wind-related disturbances can be severe and extensive, windthrow rarely has the same effect as

fire on the elimination of competing vegetation, nutrient cycling, hydrology, seedbed conditioning, and subsequent regeneration (Webb 1988, Palmer et al. 2000, Ulanova 2000). One reason for these differences is that windthrow events do not remove the biomass and expose large areas of mineral soil. Exposure to wind on exposed sites, such as ridge tops, is the major site-factor governing the potential for windthrow damage (Vitousek and White 1981). Wind damage is also a function of tree health and rooting depth and approximately linearly related to tree height (Foster and Boose 1992, Watson 2000).

The result of windthrow may often be a residual stand structure and floral mosaic that favors sprouting hardwoods rather than pine seedlings (Peterson and Pickett 1991, Peterson 2000). This mosaic is a function of the pit and mound microtopography created by windthrow. The pit and mound microsites have unique soil and microclimatic conditions that impact the regeneration process (Palmer et al. 2000, Ulanova 2000). Thus, recruitment of white pine following catastrophic windthrow may be difficult to obtain, primarily due to the rapid growth of competing hardwoods and other vegetation.

In the upper-Midwest, catastrophic windthrows may result from straight-line winds generated by strong summer thunderstorms and cyclonic winds from tornadoes. Wind events of high severity and spatial extent (e.g., July 4, 1999 storm in northern Minnesota or July 4, 1977 storm in northwestern Wisconsin) are infrequent, but can remove large patches of the forest overstory and also expose mineral soils (Webb 1988). These large-scale events may provide opportunities for tracts of white pine cohorts to become established (Canham and Loucks 1984). However, the impacts of windstorms differ across rather small spatial scales, resulting in a wide range of site conditions and thus regeneration outcomes for all species.

Hurricanes and large-scale windstorms are the primary cause of windthrow in New England and eastern Canada (Foster 1988, Peterson and Pickett 1991). The occurrence of these events corresponds with white pine recruitment across the entire region (Baldwin 1940, Spurr 1956, Foster 1988, Foster and Boose 1992). Hibbs (1983) reported that white pine comprised 50% of canopy stems on sites on the Harvard Forest affected by the 1938 hurricane. Also, Cary (1936) and Chapman (1947) attribute successful white pine recruitment to major blowdown events in New England. Severe ice

storms also have the potential to create widespread disturbance. In one case in Kentucky, midstory white pine were released from suppression by a severe ice storm that removed the overstory component (M. Smidt observation).

Disturbance frequency

Natural white pine recruitment may be an infrequent event across much of the Great Lakes region (a substantial portion of the species range), but the importance of infrequent disturbance events that favor the species over time and space cannot be underestimated. White pine refugia on rock outcrops or near wetlands and exposed areas may persist for a very long time. Old-growth stands in excess of 300 years of age have been documented (Heinselman 1996). Successful natural regeneration can be perpetuated over long periods as a result of the unique timing of disturbance events (Heinselman 1996).

The frequency of disturbance at a given site is an important determinant of the succession process (Bormann and Likens 1979, Oliver and Larson 1996). The recruitment of white pine may be facilitated by a series of low frequency, low intensity understory disturbances. For example, underburns can clear the understory vegetation, prepare a seedbed, and occasionally produce canopy gaps by killing shade tolerant conifers and fire-sensitive hardwood species (Heinselman 1981). In northern Minnesota, white pine was most abundant in locations where catastrophic fire-cycles were between 150 to 300 years. Fire cycles less than 150 years typically favored red pine (Pinus resinosa Aiton) or jack pine (Pinus banksiana Lambert), while fire cycles longer than 300 years favored succession to mixtures of white spruce (Picea glauca [Moench] Voss), balsam fir (Abies balsamea (L.) Miller), or northern hardwoods that possess greater shade tolerance (Heinselman 1981). In combination with large-scale catastrophic fires, intervening light surface fires at intervals of 20 to 40 years encourages long-term dominance of white pine (Frissell 1973, Heinselman 1981). Low intensity surface fires may also function as a natural release mechanism for white pine from suppression by fire sensitive species (Van Wagner and Methven 1978). Although white pine may also be subject to damage or mortality from these surface fires, the bark in older saplings thickens and conveys some degree of fire protection (Heinselman 1996). However,

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frequent fire events are detrimental, as Neumann and Dickmann (2001) report that a biennial burn regime dramatically reduced the presence of white pine seedlings and actually results in the recovery of abundant herbaceous cover.

Historically, fire was a major factor shaping the landscape in North America. Catastrophic fire cycles were 50 to 300 or more years with periodic light surface fires occurring between 5 to 50 years or less in the Lake States (Frissell 1973, Heinselman 1973 and 1981, Bergeron and Brisson 1990). For example in Wisconsin, 95% of the area covered with virgin forests had burned in the previous 5 centuries (Maissurow 1941). Lorimer and Gough (1988) hypothesized that these large-scale fire disturbances described by Maissurow in northeastern Wisconsin were linked to extreme drought events. Maissurow (1941) described these fires as "periodic and ecologically normal events in the life of the forest" and not as catastrophic.

Human intervention in the form of fire suppression has had a dramatic effect on pine regeneration. The pre-settlement fire disturbance cycles in northern Minnesota appear to have provided the means by which white pine was able to compete with northern hardwoods across the landscape (Heinselman 1973, Frelich and Reich 1995). The increased effectiveness of fire suppression in the last 100 years may have been a key reason for the recent lack of white pine regeneration in northern Minnesota (Heinselman 1973, Day and Carter 1990). As fire suppression increased the return time of disturbances changed and successional trends favored the establishment of more shade tolerant species such as white spruce, balsam fir or sugar maple (Acer saccharum Marshall) (Webb 1988). Under these conditions, gap-phase replacement may be the only successful avenue for white pine regeneration.

Influence of soils

Edaphic factors play an important role in white pine recruitment and growth. Soil type, fertility, soil moisture holding capacity, and topography together with climate dictate the growth potential of different species, and consequently their potential for regeneration (Husch and Lyford 1956, Mader 1986, Smith et al. 1997).

White pine grows on a wide range of soil types and conditions, and thus soil characteristics themselves are typically not considered a limiting factor (Lancaster and

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Leak 1978). Examination of recent Forest Inventory and Analysis (FIA) data confirmed that white pine is found on all soil types throughout Minnesota (A. Ek, pers. communication 1996). In Minnesota soil types associated with white pine range from fertile loess prairie soils in the south to sandy-outwash tills in the north (Prettyman 1992). Adaptation to growth on a wide variety of soils has led to the testing and selection of white pine as a reclamation species in Ohio and in parts of the Appalachians (Zeleznik and Skousen 1996, Torbert and Burger 2000). Even though white pine can be found on a range of soils, ease of establishment and growth potential vary with different soil conditions.

Typically, white pine is associated with excessively drained or well-drained sandy soils. From the Lake States to New England and Canada, soils associated with white pine cover types are characterized as glaciated alfisol-type soils (Stiell 1978). These soil types support reasonable growth rates for white pine while not being very suitable for invasions from aggressive hardwood species (Wilson and McQuilken 1963). In contrast, in the Appalachians, southeastern Minnesota, and parts of Ohio white pine grows on soils free from glaciation that are fluvial and alluvial in origin (Gaiser and Merz 1953, Francis 1979).

Soil type may influence white pine regeneration indirectly by determining the degree of competition from other trees, shrubs and herbs. Thus, without disturbance or management to reduce competing vegetation, over time the presence of white pine shifts to drier soils where competitive plants are not as aggressive (Mader 1986). Burgess and Methven (1977) describe an example of extensive white pine regeneration beneath a jack pine-red pine-white pine stand on fine lacustrine sand where fire disturbance has not played a role, but rather edaphic conditions dictate the successional state of the regeneration. Thus, edaphic factors can play a site-specific role in determining whether white pine will be self-replacing in the absence of a stand-initiating disturbance. Shallow soils derived from loamy glacial till and sandy outwash were found to support a self-replacing old growth white pine forest in Ontario (Quinby 1991). The author asserted that the main reason for this was that white pine was better able than its competitors to succeed in small canopy gaps produced by surface fires or windthrow.

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On the other hand, on more mesic sites, like old-field white pine stands in Massachusetts, sapling hardwood competition was able to completely suppress white pine advanced regeneration despite a release cutting initiated to free the pine from competition (Lutz and Cline 1947). The relative competitive ability of white pine compared to hardwood species was higher on sandier soils, as white pine cohorts were able to reach a dominant or co-dominant canopy position. On even drier sites, i.e. sandy soils, white pine regeneration was able to out compete the hardwood regeneration following release.

Clearly, a significant ecological interaction exists between edaphic factors and competing vegetation, with poorer survival and growth of the most common hardwood species on drier soils. (Ziegler 1995). Thus, the major influence of soil characteristics on white pine recruitment is through determining the vigor of competing vegetation (Horton and Brown 1960).

The influence of soil fertility on the vigor of competing vegetation will influence the optimal timing of release cuttings and thus the recruitment success of white pine. For example, on a sandy loam site that contained a well-developed hardwood understory, the established white pine had reached the sapling stage (10-38 years old) at the time of a shelterwood cutting. The timing of the release cutting combined with edaphic factors enabled the trees to compete with hardwood vegetation (Kelty and Entcheva 1993). While new white pine recruitment followed the shelterwood cutting, these seedlings were not likely to survive due to competition with regenerating shade tolerant hardwood and shrubs.

Soil type influences root development in young seedlings and thus affects potential recruitment success. Root development varies with soil depth, presence of silt or clay lenses, clay pans, nutrient availability, drainage, and soil texture (Horton and Bedell 1960, Mader 1976 and 1986, Gale and Grigal 1987, Kershaw 1993). On well-drained sites white pine develops deeply penetrating roots consisting of three to five large lateral roots with sinker roots developing from each lateral. A taproot is developed by seedlings and may not be retained over time. Moist soils and those with heavy clay pans are not conducive to healthy rooting and thus are not very suitable for white pine recruitment (Bormann and Graham 1959, Moyers 1979). Horton and Bedell (1960)

confirmed that white pine readily establishes intraspecific root grafts, which may aid in the long-term survival and health of companion trees at later stages of stand development.

Influence of Seedbed conditions

White pine seeds germinate reasonably well on a wide variety of seedbed conditions when moisture and temperature conditions are suitable (Smith 1951, Cornett et al. 1998, Weyenberg 2001). As with most conifers, bare mineral soil may be optimal for white pine and facilitates germination and early seedling establishment (Logan 1951, Smith 1951, Baldwin and Murphy 1956, Hocker 1961, Horton 1962, Van Wagner 1963, Mirov 1967, Van Wagner and Methven 1978, Duschene et al. 2000). However, in the southeast U.S., dry mineral soil may be unfavorable as a seedbed presumably due to the high surface temperatures that induce moisture stress in seedlings (Balmer and Williston 1983). In these instances, seedbeds in heavily shaded areas are conducive to germination, but incompatible with long-term seedling survival (Smith 1951), providing an example of the seed/seedling conflict sensu Schupp (1995). Lutz and Cline (1956) observed that extremely deep litter, common under mixed pine/hemlock stands, interfered with the establishment of white pine germinants. Wendel (1971) also reported that deep hardwood litter smothered first year germinants and may result in significant germinant mortality.

Several other studies suggest that herb, grass, and shrub competition with young seedlings plays a larger role in seedling establishment than seedbed conditions, indicating that what is optimal for seed germination may not necessarily promote seedling survival (Schupp 1995). Cornett et al. (1998) reported markedly increased seed and seedling survival when seed predators and competition were absent. In the study, the removal of herbaceous competition lowered mortality rates of seedlings, but did not influence germination rates.

In open areas that contained no residual overstory, competition from a range of herbs, grasses, and shrubs yielded poor white pine survival (Ahlgren 1976). In addition, seed sown in open areas had low germination (< 10% of seeds sown) but also low predation rates, while seeds sown under an herb cover had higher germination rates but also suffered higher rates of seed predation. The net result of seed predation and

competitive and environmental effects revealed that open areas produced the highest overall survival of germinants (Gill and Marks 1991).

In western Quebec, the impact of mechanical scarification of seedbeds on white pine seedling establishment and survival appeared to be the short-term exclusion of competition (Horton 1962). The benefit of scarification on seedling survival was greatest on fresh and moist sites, while on dry sites, which had low levels of competing vegetation, scarification had almost no impact on seedling establishment and growth.

Damage agents: insects, diseases, and herbivory

Consideration of biological damage agents is crucial when assessing the potential for white pine regeneration on a site. In fact, some landowners and managers have been reluctant to manage for white pine due to its susceptibility to various pests (Jones 1992). According to Wendel and Smith (1990) white pine hosts 277 insects and 110 disease organisms, a daunting array of impediments to any species. As a result, white pine regeneration has been limited in some settings, especially in Minnesota and in portions of the Lake States and Ontario. Considerable efforts have been made over the years to encourage white pine regeneration by controlling disease and insect problems, often yielding disappointing results (Bedell 1957, Cafley 1958, Coons 1978, Struik 1978, Rajala 1992, Sauerman 1992, Rajala 1998). The marginal success of many regeneration projects pushed many foresters to favor managing for alternate species that posses a higher success potential (Fowler and Heimburger 1969).

White pine blister rust and white pine weevil are two common pests that negatively affect the establishment, survival, and growth of white pine across most of its range (Cafley 1958, White 1960, Jones 1992, Katovich and Morse 1992, Pubanz 1995, Stine 1999). White pine blister rust is pandemic throughout the US and Canada, although it is much less of a problem in the southeast U.S. (Heimburger and Holst 1955, Garrett 1986, Zuffa 1986). Landscape position and microclimate conditions greatly affect the incidence of blister rust infection rates (Van Arsdel 1972, Hunt 1997). Thus, disease management strategies recommend against attempting regeneration of white pine in locations identified as "high risk" zones, typically areas characterized by cool moist habitats where there is air movement to transport the disease spores or high humidity

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conditions in the lower branches with little air movement (Robbins et al. 1988, Hunt 1997). Recent strategies have focused on creating conditions unfavorable for the transmission of the spores (Van Arsdel 1962, French 1992). One common method is to establish white pine under an overstory canopy, which intercepts light and reduces air movement which results in modified ambient heat flux and moisture patterns needed for transmission of the spores (Van Arsdel 1962, French 1992). White pine regeneration may also benefit from appropriate pathological pruning and/or local Ribes eradication programs designed to remove the alternate host for the disease (White 1960, Lehrer 1982, Gross 1985b, Hunt 1991, Stine 1999).

The white pine weevil is a native insect that rarely causes mortality, but can cause significant growth and economic losses by deforming terminal leaders on young trees (Graham 1918, Morrow 1941, Waters et al. 1955, Stiell 1968, Brace 1971, Berry and Stiell 1976, Gross 1985a). Larvae feeding in the terminal branch girdle the inner bark causing wilting and death of the leader, and in severe cases the loss of up to two years growth (Berry and Stiell 1976, DeBoo 1978, Katovich and Morse 1992). The direct result is loss of tree vigor, height growth reduction and wood quality as the tree responds with multiple stems and/or significant sweep (Waters et al. 1955, White 1960, Spurr and Friend 1965, Brace 1971). Height growth reduction further exposes seedlings to increased browse potential and overtopping by competing vegetation.

Weevils seem to prefer to infest trees with thicker terminal leaders, such as those found in vigorously growing trees (Sullivan 1961, Berry and Stiell 1976, DeBoo 1978, Drooz 1985, Garrett 1986, Katovich and Morse 1992). Micro-environmental conditions in an understory environment, such as reduced light levels, are considered detrimental to all stages of weevil development (Katovich and Morse 1992, Lavallée et al. 2001). Thus, white pine regeneration under an overstory tree canopy is usually less prone to damage from weevil infestations. For example, where light transmission to the forest floor was reduced by 25-50%, damage caused by white pine weevil was reduced to one-tenth of that for open-grown trees (Berry and Stiell 1976, Stiell and Berry 1985). Pubanz et al. (1999) concluded that weevil injuries that affect pine stem form have been pandemic for the last 150 years. While chemical controls represent an effective means to control

weevils, the costs, restrictive federal policies/regulations, and public opinion pressure have limited this silvicultural practice to selective sites (DeBoo 1978).

Genetic improvement programs for white pine aimed at producing weevil and blister rust resistant trees continues (New Hampshire Forestry and Recreation Commission 1956, Fowler and Heimburger 1969, Anderson 1973, Ledig and Smith 1981, Hubbes and Lin 1985, Zsuffa 1985, Garrett 1986, Zsuffa 1986, Blada 1989, Meier 1992, Stine 1999). However, the long-term nature of genetic research ensures that these pest problems will continue to affect white pine in the foreseeable future.

Deer herbivory on white pine is a significant source of seedling mortality, loss of growth, and reduced tree vigor (Stiell 1978, Whitney 1984, Alverson et al. 1988, Gill and Marks 1991, Sauerman 1992, Tester et al. 1997, Saunders and Puettmann 1999a and 1999b, Ward et al. 2000). Deer depredation also prolongs the period that seedlings are within reach of deer. Repeated browsing is quite common and especially detrimental (Saunders and Puettmann 1999a, Saunders and Puettmann 1999b). Because of public interest in large deer populations and the abundance of favorable habitat, widespread reduction of the deer population to historic levels is not likely. Herbivory by small mammals, especially rabbits, can be intense during winter months and can result in levels of mortality and growth loss equal to those from deer (Aldous and Aldous 1944, Stiell 1978, Giusti et al. 1992). Intense herbivory over protracted time periods may alter successional pathways and favor single tree recruitment.

Small mammal (squirrel, mice, vole, chipmunks) seed depredation and seedling predation has the capacity to limit white pine recruitment (Abbott 1961, Graber 1969, Abbot and Quink 1970, Gill and Marks 1991, Heckman 1992). Field mice (Peromyscus sp.) can have such a profound impact and in areas with high mice populations could limit the success of forest regeneration in general (Abbott 1961). Duchesne et al. (2000) found white pine seeds to be a preferred food source for small mammals. Conversely, white pine seedling recruitment in a mixed forest that includes a component of oak or hickory may actually be increased due to the digging and seed cache creating activities of small mammals such as squirrels and chipmunks (Alexander et al. 1986). Graber (1964) found that the white pine cone beetle (Conophthorus coniperda (Schwarz) (Col., Scolytidae)) could dramatically decrease seed availability in local areas.

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Defoliating insects may intermittently cause extensive damage affecting seed tree vigor and regeneration of white pine in localized areas. Members of the sawfly genera that include the white pine sawfly (Neodiprion pinetum Hartig) and the introduced pine sawfly (Diprion similis Hartig) occasionally infest foliage resulting in mortality (Houseweart and Knight 1986). The gypsy moth (Lymantria dispar L.) is primarily a defoliator of hardwoods, but is known to feed on white pine in the northeast US (DeBoo 1978, Stiell 1978, Drooz 1985, Katovich 1992). In the southeast US, pales weevil (Hylobius pales Boh.) causes mortality (up to 100%) in seedlings grown on cutover lands (Moyers 1979, Houseweart and Knight 1986). The pine leaf adelgid (Pineus pinifoliae Hartig) has been identified as a cause of mortality and loss of growth on research plots in northern Minnesota (J. Krueger field observation).

A number of fungi cause mortality and growth loss in young white pine. These include Armillaria root rot (Armillaria mellea [Vahl ex. Fr.] Kumm.), red rot (Fomes pini [Thore ex Pers.] Lloyd) and white pine root decline (Verticicladiella procera). These fungi are primarily associated with merchantable volume loss, but can certainly play a role in reducing the vigor of seed trees and thus cause reductions in seed production (Ostrander and Foster 1957, White 1960, Gross 1985a). Annosus root rot (Fomes annosus (Fr.) Karst.)), a root and butt-rot fungi is known to cause merchantable losses in plantations undergoing frequent thinning and can similarly play a role in the potential for seed production (Walker 1967). Stand mortality from these pests is intermittent and usually only trees weakened through other means are killed (Gross 1985a).

Influence of management decisions

Ongoing anthropogenic changes to ecological processes at the landscape level, especially since European settlement, have significantly impacted regeneration dynamics in temperate forests (Williams 1989). These changes provide challenges to forest managers who work to return white pine to a semblance of its former role as an important ecological component of the forest. The willingness and ability of forest managers to re-enter a stand at different critical life stages with the intent to implement protection measures or manipulate vegetative composition that favors white pine, will directly impact the level of regeneration success. This consideration is especially critical where

white pine is being regenerated on high productivity sites where the competitive regime is intense or there are significant herbivory challenges.

To obtain adequate stocking levels and promote survival of seedlings in situations where white pine is recruited under a dense canopy or understory cover, release mechanisms must eventually be implemented to reduce mortality resulting from suppression. This is especially true where regeneration attempts are made in mixed conifer-hardwood stands where the initial slow growth of white pine puts it at a competitive disadvantage. White pine can survive for many years in the understory with limited light conditions and responds well to release after nearly 40 years of suppression (Kelty and Entcheva 1993). The capacity to survive suppression for many years and yet exhibit strong growth patterns following release provides flexibility to forest managers. In most cases where white pine is overtopped some release mechanism is required to ensure that suppressed white pine will reach the overstory (Machado 1999). Because of dramatic changes in disturbance events and frequencies in temperate pine forests since human settlement, managers should analyze seedbed conditions at the time of seedfall. Seed year quality and quantity is typically monitored by various public agencies and recruitment is generally enhanced when foresters deliberately combine exposure of mineral soils and reductions in competing vegetation with good seed crops.

Ownership fragmentation of the landscape has created a number of management challenges to forest regeneration (Perera and Baldwin 1993, Frelich et al. 1998). Land clearing for settlements, agriculture, and logging all contribute to ownership patterns that result in smaller stand sizes (Mladenoff et al. 1993, Leatherberry 1998, Schmidt and Raile 1998, Gobster et al. 2000). As forest fragmentation increases and land ownership patterns change, so do landowners objectives (Gobster et al. 2000). Relatively long rotation requirements for white pine compared to other species combined with pest and disease problems may discourage many owners from managing for white pine (Bennett 1986). Shorter rotation species such as aspen or less problematic species such as red pine may be more appealing. Land clearing operations also contribute to increasing deer populations by creating improved deer habitat and result in subsequent problems with herbivory (Whitney 1984, Alverson et al. 1988).

Fire suppression is one of the main reasons for the widespread ecological changes in the structure and function of temperate forests (Candy 1939, Ahlgren 1976, Heinselman 1981, Whitney 1984, Clark 1990, McRae 1994, McKenzie et al. 1996). White pine has been repeatedly described as a fire dependent. Natural fire rotations or implementing silvicultural activities that mimic fire are increasingly difficult for land managers to achieve (Plevel 1997, Lichtman 1998). Changes to disturbance regimes considered essential to white pine regeneration can limit opportunities to manage for the species. Limited finances to implement prescribed burns, public concern about fire control, and/or the application of herbicides severely limits management options. Mechanical site preparation or release is an available tool to promote regeneration opportunities, but these measures are labor intensive and likely more expensive than utilizing naturally occurring mechanisms such as overstory retention and may not always be as effective (Miller 1978, Clinton et al. 1997). In addition, practices like mechanical site preparation are under scrutiny as forest managers aim to limit soil disturbance (Smith et al. 1997).

Management considerations can become extremely complex in light of changing societal expectations for natural resource managers. Policy considerations that include preservation of old growth stand elements, cultural significance, multiple use management, reduction in the reliance on public lands as a source of wood fiber, and the increasingly conflicting viewpoints of advocacy groups all add to the complicated management process (Schroeder 1992, Tlusty 1992). The interplay and relative significance of these factors may discourage certain silvicultural operations (e.g., herbicide applications), aimed at expanding regenerations efforts.

Examples of Integration Scenarios

All of the factors reviewed interact to determine regeneration outcomes. The exact nature of the links and strengths of the interactions varies across the landscape and with the management scenarios. To illustrate how these interactions influence regeneration, I draw on two examples of common management practices for white pine, clearcut and shelterwood. These examples demonstrate the complexity of factors (both positive and negative) and interactions managers should consider to influence

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regeneration outcomes. Following is a short description of the factors and their interactions as highlighted in Figures 1.2a and 1.2b for clearcut and shelterwood reproduction methods, respectively.

The Clearcut Method

The clearcut method remains common in the Lake States and results in the most dramatic shift in ecosystem conditions and dynamics. Typically clearcutting is associated with site preparation (through harvesting and separate site preparation treatments) and likely (but not necessarily) artificial regeneration. White pine is often successfully managed in this manner, and if successful clearcutting results in the establishment of an extensive even-aged cohort of white pine.

The clearcut method removes the overstory structure and results in a number of ecological changes. Figure 1.2a shows that the disturbance associated with clearcutting usually results in little or no seed availability on the site. To ensure seed availability the harvesting operation should be timed to coincide with ripe seeds on the trees. An alternative is to harvest following natural seed dispersal or disperse seed manually across the site. Follow up treatments, such as site preparation, have to ensure survival of seeds or young seedlings, e.g., broadcast burning may not be appropriate. Ecological impacts that result from this method include: changes to plant structure and composition, soil compaction, alteration of the local hydrologic cycle, erosion, nutrient cycling, and impacts on microclimate and soil micro-fauna populations (Smith et al. 1997). Mineral soil exposure which results from the harvest operation modifies seedbed conditions and likely results in improved germination success.

The competitive regime is altered significantly, as clearcutting completely eliminates competition from overstory trees. However, on most sites, additional site preparation and release treatments are necessary to reduce competition from shrub and herbaceous layers to ensure white pine growth and survival. These changes in vegetation also affect other components of the ecosystem and may result in increased or decreased potential for seedling damage. For example, opening a stand and the rapid response of vegetation may attract animals that browse white pine. Similarly, opening the stand often results in increased incidence rates for white pine blister rust, pine bark adelgids, and

white pine weevils. On the other hand, the potential loss due to fungi, such as damping-off, may be reduced in the drier microclimate in clearcuts.

The Shelterwood Method

The goals of the shelterwood and clearcut reproduction method are generally similar: the regeneration of even-aged fully stocked stands. The shelterwood method is generally chosen because of the need to protect seedlings in harsh environments and because of other benefits of residual structure, such as reduced visual impacts. However, a detailed analysis of the integrated regeneration dynamics (Figure 1.2b) shows a number of differences between the clearcut and shelterwood reproduction method. In shelterwood management, the harvest is less intensive, as only a portion of the trees are removed at a time. Since multiple entries are necessary, repeated disturbance of the understory vegetation will have some negative impact on the established white pine regeneration. In some stands, the potential for windthrow or breakage of residual overstory trees may increase after the seed cut and may result in patchy disturbance and recruitment patterns.

Retaining white pine in the residual canopy will increase chances of seed availability in shelterwoods. Seed trees are generally selected for their vigor and large crowns. Timing the harvest in a good seed-year is still very important (see discussion for clearcuts). However, since the seed source is still present on the site, a failure of natural regeneration in the year of harvesting may only delay the advent of regeneration till the next good seed-year. This may require repeated site preparation treatments, depending upon the decay rate for seedling safe sites.

Multiple stand entries raise concerns about soil compaction and alteration of hydrological regimes. However, the extent of the disturbance (assuming a designated skid trail system) is usually less than in clearcuts. Also, the impact may be less dramatic due to the impact of residual stand structure. For example, root strength of the residual trees will help stabilize slopes. Also, the disturbance events are spread out over time allowing for site recovery. As in clearcuts, harvest operations usually improve seedbed conditions for natural regeneration. While conditions of soils are not as crucial, the shelterwood

may provide better microclimate conditions for germination and early establishment by being cooler in summer, and less prone to frost.

Competitive conditions for white pine seedlings are improved through the harvest operation and also through the dampening effect from the remaining canopy. Competing understory vegetation may not be as aggressive due to the influence of overstory trees. However, the overstory trees compete directly with the seedlings, resulting in lower growth rates. Thus, the need for site preparation and release treatments as a means to reduce competition varies with the overstory conditions.

The residual overstory benefits the seedlings by altering the microclimate and moisture conditions and thus reducing the quality of habitat for various pests and diseases. For example, the incidences of white pine blister rust, white pine weevil, and pine bark adelgids are lower in understory conditions. On the other hand, the slower growth rates for seedlings in understories means that they will be in high risk conditions longer, as risk for blister rust infections and deer herbivory decreases with increasing seedling size.

Conclusion

A host of integrated biotic and abiotic factors drive white pine regeneration patterns across the landscape. Land managers challenged with utilizing scarce resources in an effort to increase the presence of white pine must consider the specific influence these factors have, how they are interacting, and how management actions influence these interrelated factors. I selected six factors that drive regeneration outcomes within the natural range for white pine and examined their impacts and interactions regarding the regeneration process.

For each factor, I reviewed the literature to highlight ecological relationships and the influence on the regeneration of white pine. These factors are interrelated in a number of possible combinations and it is this integration that determines the regeneration outcome. Thus, in assessing potential recruitment outcomes and management options, the impact of any one factor should be considered within the full suite of site conditions. This approach can provide a reference for managers by outlining the range of factors and interactions that influence regeneration success and thus can help

avoid management decisions being driven by single factor analysis. This method promotes flexibility through consideration of options/alternatives and attempts to minimize risk associated with planning regeneration operations. Two common reproduction methods provide examples illustrating the complexity of factors and interactions that are altered by the decision to shift from clearcutting to using the shelterwood method. Using an integrated approach to assessing regeneration illustrates the need to further research ecological links associated with changing stand dynamics, forest practices and regeneration strategies.

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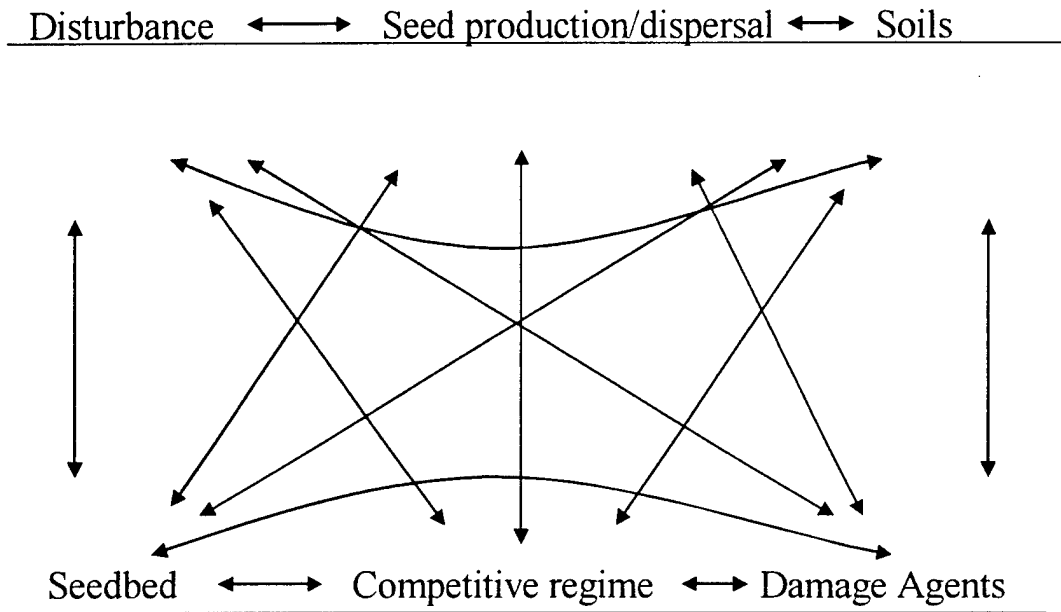
Figure 1.1 Conceptual model of the potential interactions among disturbance, seed production and dispersal, soils, seedbed, competition and damage agents. Both the significance of the factor and the strength of the relationship to other factors may vary considerably. The interactions may be positive, negative or neutral.

Disturbance ──→ **Seed Production/Dispersal** ←── **Soils**

-harvest initiated.
-compounded by additional stand entry.
use of herbicides.
-may impact advanced regeneration

-managed change to residual seed trees and thus future stand composition and structure.
-planting or seeding is alternative.
-timing critical to take advantage of standing seed crop.

-compaction due to harvest.
-modified micro-flora/fauna.
-fertile soils may drive competitive recovery.
-potential erosion increased.

Seedbed ──→ **Competitive Regime** ←─→ **Damage Agents**

-highly modified by the sequence of disturbances, mineral soil exposed.
-residual litter/O-matter impacts germination. soil moisture and surface temperature fluctuations.

-disturbance minimizes early interspecific competition. seedling density will influence intraspecific competition.
-may create opportunity for aggressive shrub and herbaceous plant growth.

-density dependent threats reduced.
-can create preferred browse.
-increased incidence rates for blister rust/adelgids/weevils likely.
-increased root rot pathogens from decaying materials.

Figure 1.2a Relative significance of the interactions associated with the clearcut reproduction method. The relative significance of the relationship between individual factors is defined by both the thickness of the line and positive (+), negative (-) indicators or neutral (no indicator).

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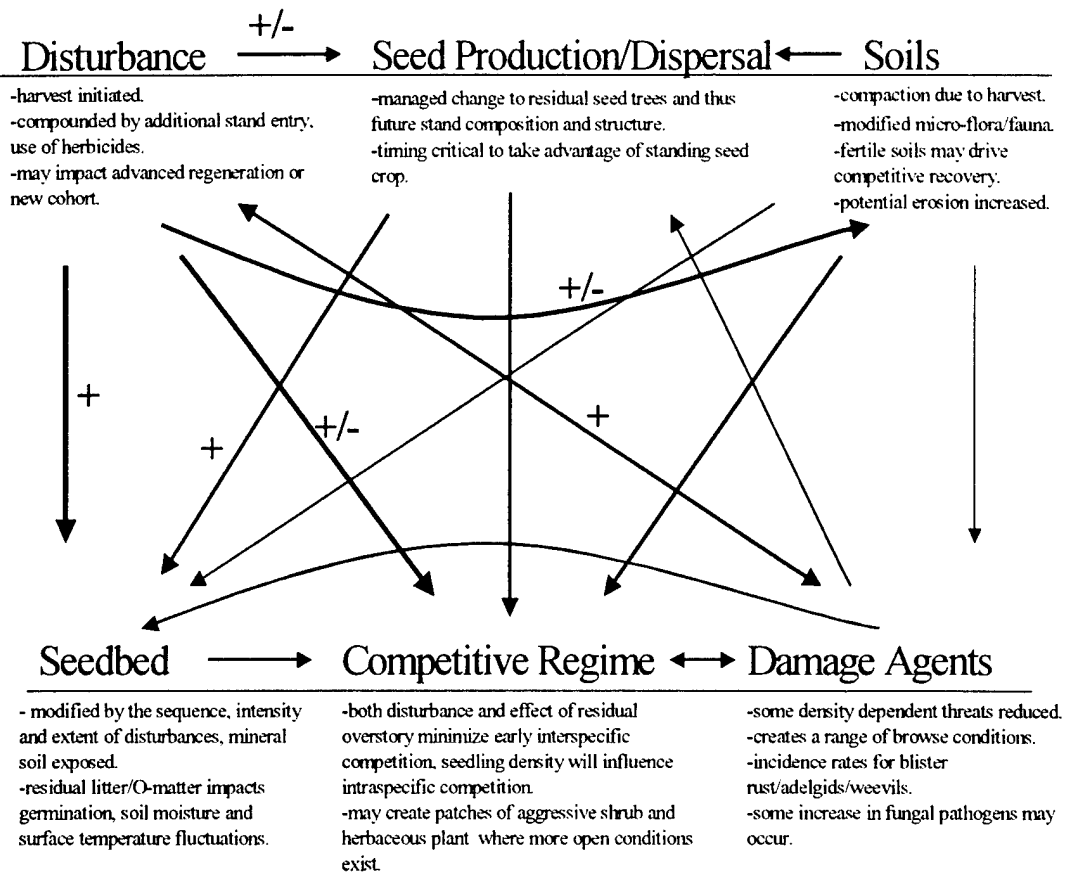
Figure 1.2b Relative significance of the interactions associated with the shelterwood reproduction method. The relative significance of the relationship between individual factors is defined by both the thickness of the line and positive (+), negative (-) indicators or neutral (no indicator).

CHAPTER 2

Growth and injury patterns of eastern white pine (*Pinus strobus* L.) seedlings as affected by hardwood overstory density and weeding treatments

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Growth and injury patterns of eastern white pine (*Pinus strobus* L.) seedlings as affected by hardwood overstory density and weeding treatments

Abstract

White pine seedlings were underplanted under a range of overstory densities in a hardwood stand in northern Minnesota, USA. Woody and herbaceous vegetation surrounding seedlings was left untreated (control), weeded annually or completely removed through monthly weeding. After four years, the benefit of weeding for diameter growth of seedlings was limited to areas with relatively open overstory conditions. Seedling height growth was reduced in areas with higher overstory density, but improved through weeding treatments. The removal of herbaceous vegetation did not improve growth of seedlings in any conditions. Open growing conditions created by overstory removal and weed control resulted in higher incidences of seedling injuries, e.g., through infection by white pine blister rust. Conditions for pine bark adelgids also were enhanced in areas with low overstory densities and in weeding treatments. The incidence for white pine weevil seems to follow a similar pattern, although the number of trees infected was minimal. Results show that improving growing conditions through decreasing the overstory and understory vegetation improves seedling growth rates, but also risks increasing the incidences of seedling injuries under more open conditions. Increased risk for damage may impact the recruitment outcome by altering seedling stocking levels.

Introduction

Over the last decade, harvesting operations in Minnesota, much like in other parts of the U.S. and Canada, have exhibited a trend toward the increased retention of residual trees (green tree retention) (Puettmann and Ek 1999). Typically, this practice is not aimed at providing optimal conditions for regeneration, but to fulfill other objectives, like riparian protection, wildlife habitat, or visual quality. Thus, green tree retention results in residual stands unique from those subject to the practice of clearcut and shelterwood systems or those affected by natural disturbance (Franklin *et al.* 1997, Halpern *et al.* 1999). The implications of this practice, especially for regeneration and younger cohorts are as yet uncertain (Acker *et al.* 1998). These remnant vertical structures influence the regeneration process, thus increasing the need for understanding how understory vegetation, including tree regeneration, responds to conditions created by different overstory and understory conditions. Gaining an improved understanding of stand dynamics under these conditions may provide insight into silvicultural treatments that optimize the benefits of green tree retention while minimizing negative effects of interspecific competition (Palik *et al.* 1997).

A number of studies have documented white pine seedling response to ranges of light conditions (Shirley 1945, Logan 1966, Messier *et al.* 1999) and to vegetation management (Freeman and Van Lear 1977, Brand and Janas 1988, Cornett *et al.* 1998). Few studies have documented the integrated effect of over- and understory vegetation management on subsequent white pine seedling growth (Smidt and Puettmann 1998, Wetzel and Burgess 2001). The objective of this study was to gain insight into the role that harvesting intensity and vegetation management play in early growth response of underplanted white pine. The specific objectives were to (1) quantify the growth response of planted white pine to a range of overstory hardwood densities, (2) evaluate the impact of understory vegetation management practices on early seedling growth, (3) separate the effects of different vegetation components (overstory, shrub and herbaceous vegetation) in terms of their influence on seedling growth during years 2 and 4 after planting, and (4) document how white pine seedling injury patterns are influenced by overstory and understory conditions.

Study Area

The study site was located 12 km northwest of Two Harbors, MN, U.S.A. in southern St. Louis County (approximately 47°04′N, 91°51′W: Altitude = 420 m asl). The 5.4 ha site lies on flat terrain with a few scattered shallow depressions. Soils are an outwash derived, well drained medium/sandy-loam in the Normanna-Canosia soil series (57 % sand, 33 % silt, 10 % clay). A soil macronutrient analysis was conducted at a central location at 0-15 cm and 16-30 cm depth (Table 1). Due to the relatively low relief across the site and the consistency of the soil series and cover types, it is unlikely that nutrient conditions varied substantially across the site. The climate is considered to be mid-continental, with mean January temperatures of –11 °C and a mean July temperature of 18 ° C. Mean cumulative growing season (April to August) precipitation is 42 cm of rain (Two Harbors meteorological station, MN State Climatology Service).

In the summer of 1994, a diameter-limited thinning operation was conducted across the site using a mechanical harvester and full tree skidding to a central landing. The thinning operation was designed to create a range of residual overstory conditions. The resulting residual overstory conditions ranged from relatively open (basal area (BA) 4m²/ha) to relatively dense (BA 22m²/ha).

The post-thinning stand was comprised of an approximately 70-year-old overstory dominated by sugar maple (*Acer saccharum* Marsh.) (45% of basal area) and paper birch (*Betula papyrifera* Marsh.) (29% of basal area) with scattered basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britton), aspen (*Populus tremuloides* Michx.), ash (*Fraxinus* sp.), white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill). Average tree height was 17 m, average diameter was 23 cm, and total overstory basal area averaged 11 m²/ha. The understory consisted of dense patches of regenerating hardwood stems, especially sugar maple, raspberry (*Rubus* spp.), blackberry (*Rubus* spp.), and beaked hazel (*Corylus cornuta* Marsh.). Common herbaceous species included big leaf aster (*Aster macrophyllus* L.), braken fern (*Pteridium aquillinum* (L.) Kuhn.), bunchberry (*Cornus canadensis* L.), and sweet scented bedstraw (*Galium triflorum* Michx.).

Experimental Design

In April 1996 24 rectangular plots (approximately 85 m^2) were established across the site with the goal of covering the full range of overstory density conditions (BA). Plots were located randomly within the overstory density constraints. The plots were placed a minimum of 14 m apart and skid trails were avoided. Thirty-six bare root seedlings (3-0) were planted in each plot (6 rows X 6 seedlings/row, 867 total, 3 rows received one extra tree). Seedling spacing was 1 m within rows and 1.5 m between rows. In an attempt to mitigate the impact from herbivory, seedlings were grown in plastic mesh cages through April 1998 (Ward *et al.* 2000). Following the removal of the mesh cages paper bud caps were used to protect terminal leaders during the following two winters.

Weeding treatments were randomly assigned to rows of seedlings. The weeding treatments were (1) control (no removal of competing vegetation), (2) annual (single removal of understory vegetation in early June) or (3) monthly weeding (understory vegetation was removed monthly during the growing season). The weeding treatments were applied in a 1 m swath centered on the rows during all 4 years. The weeding treatments were accomplished using a nylon line equipped gas powered weed trimmer and hand removal.

Measurements

Percent cover of shrubs and herbs that were taller than ½ the seedling height within 1 m of each target tree were estimated visually in the second and fourth growing season following planting (1997 and 1999). To ensure consistency in the estimations the same observer conducted estimates in each year. Light extinction (and by extension resource uptake and associated environmental conditions) by the overstory was quantified using the LICOR LAI2000 in summer 1997. Light readings were taken directly above the terminal leader for each seedling on an overcast day following the method proposed by Saunders and Puettmann (1999a). The LAI calculates diffuse non-interceptance (DIFN), an indicator of canopy structure or openness (*sensu* Saunders and Puettmann 1999a) and is an unbiased predictor of average growing season light transmittance (Comeau *et al.* 1998, Gendron *et al.* 1998). The DIFN values for all weeded seedlings (i.e., with no overtopping herbs and shrubs) were averaged by plot and used as a means to

characterize growing conditions as modified by overstory trees. Overstory basal area (BA) was measured by a prism count (1 m^2 BAF) in the center of each plot and used as a second metric for overstory canopy density. There is a close correlation between the DIFN and plot level BA values, with BA being a commonly used metric to characterize stand density, while DIFN represents a more physiological approach related to light availability, but includes factors associated with canopy openness (Comeau 2001, Puettmann and D'Amato in press).

Tree seedlings were measured in fall of 1994 and every fall thereafter until 1999. Measurements included total height, basal diameter (at 5 cm, hereafter referred to as diameter). At the time of measurements, I noted the source (where identifiable) of any damage or reason for mortality. While seedlings were not measured at the time of planting, they were selected for homogenous size and the planting sequence was random. Thus, I assumed that seedling size was not different at the time of planting and subsequent size differences were due to growth differences after outplanting. Height and diameter values were averaged by row and size after four growing seasons was used as an indicator of early seedling growth.

The incidence of herbivory, insect and disease were assessed though the fifth year following planting. Animal damage, mainly rabbit and deer browsing, during the 1999/2000 winter reduced the sample size and in the fall of 2000 measurements were limited to identifying the cause of seedling mortality.

Data analysis

SAS Version 8, (SAS Institute Inc., Cary NC) was used to construct and test statistical models. All tests were considered marginally significant if $p < 0.10$, significant if $p < 0.05$, and highly significant if $p < 0.01$. Model construction was accomplished under the direction of Ms. C. Davey, University of Minnesota Biostatistics Laboratory.

Analysis of covariance (ANCOVA) was used to test objectives 1 and 2 for the effect of an overstory density gradient (overstory basal area (BA)), categorical weeding treatments (WEED), and their interactions on total height and diameter in year four. The Least Squares Means test (LS Means) was used to correct for unbalanced data parameters. The Bonferroni (Dunn) t-test approach for multiple comparisons was used to

prevent the inclusion of any false significant differences related to weeding treatments (Rosner 1982).

Multiple linear regression (MLR) was used to test objective 3. The model tested the effect of herbaceous and shrub cover and DIFN (as influenced only by the overstory) and all possible interactions on seedling growth during years 2 and 4. Since the assumption of similar seedling size at the beginning of the growing seasons was not valid after the first growing season, initial size (height after 1 or 3 years, diameter after 3 years) and possible interactions were included into the models. Residual analysis was used to determine whether model forms were appropriate. No transformation of the variables was warranted (C. Davey, pers. communication).

Logistic regression was used to investigate the general relationship between BA and WEED on the incidence of three common diseases/pests: white pine blister rust (*Cronartium ribicola* J.C. Fisch.), pine bark adelgids (*Pineus strobi* Hartig), and white pine weevil (*Pissodes strobi* Peck). Due to the limitations of the data set based for determining incidence rates, inference on specific relationships is limited.

Results

Effect of overstory density and weeding treatments on four-year height and diameter growth

Analysis of covariance (ANCOVA) identified overstory density (BA) and weeding treatments (WEED) as significantly influencing four-year height and diameter growth of white pine seedlings (Table 2). In general, seedlings responded to decreasing overstory density and the removal of competing vegetation with increased growth, both in height and diameter (Figures 2.1a and 2.1b). There was no interaction between BA and WEED for 4-year height growth, but a significant interaction between BA and WEED exists for diameter growth (Table 2). Sensitivity to understory vegetation was indicated for diameter growth with the development of a significant interaction WEED*BA.

Vegetation removal resulted in trees that were significantly taller across the range of basal area examined (Figure 2.1a). Mean height was 93.4 cm ± 3.1 for trees receiving annual weeding and 96.1 cm ± 3.1 for trees receiving monthly weeding. These means differ significantly from that of control trees, which averaged 68.5 cm ± 3.1. Seedling

diameter growth benefited from weeding under open overstory, but not under dense overstory canopies where DIFN values were appreciably lower (Figure 2.1b). Overall, diameter for annual and monthly weeded trees averaged 13.19 mm ± 0.47 and 14.26 mm ± 0.47, respectively, while control tree diameter averaged 7.55 mm ± 0.48. Bonferroni (Dunn) and LS Means tests revealed that the height growth response to annual and monthly weeding treatments were significantly different from seedlings in the control rows, but not significantly different from one another. A visual analysis of Figure 2.1b suggests that diameter growth patterns also follow this trend.

Separating the effects of overstory, shrub, and herbaceous cover on seedling growth in the second and fourth year

My analysis here is aimed at exploring the results from the previous section in greater depth by using detailed assessments of understory vegetation cover taken in the summer of 1997 and in 1999, i.e. 2 and 4 years after outplanting. The response variable examined is the annual growth (diameter and height) as influenced by four factors (initial height or diameter, herb cover, shrub cover and DIFN)(Table 3). As expected, initial height and DIFN are highly significant predictors of height growth in year 2 (p<0.0001). However, the interaction between initial height and DIFN was not statistically significant (p=0.78). Thus, in year two, a 10% increase in the DIFN level (i.e. a tree grown under more open conditions) results in an increased height growth of 1.1 cm holding other model values constant. By the fourth year significant interactions had developed between DIFN and the seedling initial diameter and height (Table 3). Overstory conditions strongly influenced seedling growth during the first three years, and consequently seedlings under higher overstory densities were smaller in the beginning of year 4. Shrub cover, by itself in the second year and in combination with DIFN by the fourth year was highly significant. In the second year, an increase in shrub cover of 30 % (i.e. associated with more open conditions) would be associated with a decrease of 1.2 cm of height growth and 3 mm in diameter growth. By the fourth year, the same increase in shrub cover results in a decrease of 3 cm of height growth and 1 mm in diameter growth. (DIFN values set to 0.4 and 0.3 respectively).

A second, highly significant interaction developed between shrub cover * DIFN for year four diameter growth. Under open overstory conditions (high DIFN), increasing

shrub cover will lead to reduced seedling growth, while under dense overstory conditions, the seedling growth response to increasing shrub cover is essentially flat (Figure 2.2). This suggests that plots with lower overstory densities have both higher initial diameters and a greater abundance of competing woody vegetation, which in turn is correlated with the growth of the seedlings in year 4 (Figure 2.2).

Herb cover was marginally significant as a predictor of height growth in year two but by the fourth year was not statistically significant for height or diameter growth (Table 3). Even in year 2, the practical importance of herb cover is minimal. For example, in the second year a 10 % increase of herb cover results in a 2 mm decrease in height growth. By year four, a similar increase in herb cover results in a decrease of diameter growth of 0.4 mm.

Injury patterns: Herbivory, Disease, and Insects

Herbivory was the major reason for the termination of the experiment. Over the five years, 377 (43%) of seedlings were subject to terminal browse and 728 (84 %) had some lateral browse. In the final year the number of viable seedlings dropped from n = 556 to n = 262 , with 5 of 24 plots no longer having any viable seedlings. This reduction was primarily a function of herbivory by deer and rabbits.

During the study period, white pine blister rust was not a major source of mortality. Cankers on stems or lateral branches were observed on 102 trees (12 %). Nearly twice the proportion of trees (13.3%) were infected in weeded rows compared to those in control rows (7.6%) (Figure 2.3). The logistic regression model indicated that BA and WEED are significant predictors of rust infection at this site.

Pine bark adelgids were present to some degree across the entire site. A total of 127 trees (15%) were observed to have some level of infestation. Almost all (91%) occurred in rows with active vegetation removal. Trees in weeded rows had an infestation rate nearly five times higher than trees in control rows, 19.8% vs. 3.8% (Figure 2.3). Using logistic regression, both BA and WEED were significant in predicting the probability for adelgid infestation. As the level of BA decreases and vegetation removal occurs, the probability for infestation increases. No specific instances of dieback, loss of growth or vigor were observed as a result of adelgid presence on seedlings.

Another pest of white pine in Minnesota, white pine weevil, appeared to have little impact at this site. Although I did not specifically check for the presence of weevils, I assumed that the terminal leader dieback that is typical for white pine weevil attacks, indicated infestation (Drooz 1985). This condition was observed only on 15 seedlings (2%) in five years. Due to the small number of trees infected I could not test statistically whether terminal dieback occurred on plots that were more open. However, only 1 of 15 (7%) proposed weevil attacks occurred in control rows with denser cover over seedlings. Proportionally 0.7% of control trees exhibited weevil symptoms versus 2.3% of those in weeded rows (Figure 2.3).

Other factors, such as windthrow, which may have occurred after opening up the stand, apparently were not influencing seedling vigor and survival. While a number of overstory trees did subsequently blow down, no widespread windthrow occurred. A single seedling was killed due to an overstory tree falling on it.

Discussion

My results support the hypothesis that there is a significant, quantifiable relationship between overstory density, understory competition and the growth response of white pine seedlings. A negative relationship existed between overstory density and seedling diameter and height growth for the range of overstory densities present in my study site. This is very similar to results reported by Smidt and Puettmann (1998) who studied the growth response of white pine up to 10 years after planting in stands with varying vertical structure, composition, and vegetation management in northern Minnesota. My study supports their findings that under relatively open overstory conditions, the understory cover represented the dominant competition for white pine seedlings. On the other hand, where dense overstory conditions exist, there is a discernable dampening effect, as understory is less competitive. Consequently, under denser canopy conditions, weeding treatments have a smaller effect, most likely due to the suppression effect that canopy closure has on both the competing species and the seedlings (Riegel et al. 1992, Smidt and Puettmann 1998). Wetzel and Burgess (2001) reported similar results for early growth in white pine if brush control was combined with overstory thinning (1 to 2 crown spacing) and blade scarification.

Shrub cover response following the harvest appeared uniformly aggressive across the site irrespective of overstory basal area coverage (data not presented). I assessed by weeding treatments (which included removal of woody materials), the impact of shrubs on white pine growth was greatest where overstory densities were lowest. In those conditions, I found that seedling height and diameter growth were negatively correlated with shrub cover. Conversely, Saunders and Puettmann (1999a) found that brush control treatments strongly affected seedling diameter, but not their height growth. This difference may be attributed to differences in vertical structure of the shrub layer, vegetation removal techniques, and differences in the ages of seedlings studied.

Conversely, the presence of dense understory vegetation may support favorable outcomes. Retention of competing shrub cover and higher levels of overstory densities seemed to provide protection from blister rust as reported by several authors (Van Arsdel 1962, Lancaster and Leak 1978, Katovich and Morse 1992). I observed a similar response with the incidence of pine bark adelgids, which were nearly absent under the heaviest competition levels in control rows. In addition, shrub cover provides hiding cover for juvenile white pine that once exposed as a result of vegetation removal may be subject to severe browse (Saunders and Puettmann 1999b).

Herbaceous competition did not exhibit a significant influence on seedling growth patterns (height or diameter growth) through the fourth year. This is likely due to the use of manual weeding treatments, which set back any herbaceous vegetation each season. Where herbaceous cover recovered quickly, they may not be as competitive as undisturbed herbaceous vegetation (with the same percent cover). The competitive impact in year 2 is statistically significant. However, because of the small absolute impact, it is of low practical importance. Harrington et al. (1995) also points out the ability of herbs to expand when shrubs and tree cover were reduced by release treatments. Various authors (e.g., Wagner et al. 1996 and 1999, Bell et al. 2000, Zutter et al. 1998) reported that herbaceous competition significantly impacts height and diameter growth of seedlings for up to five years. For example, Wagner et al. (1996 and 1999) reported a decrease in stem growth rate of 20% after a single year of exposure to herbaceous competition. The discrepancy in the importance of herbaceous competition between these studies and this one may be due to difference in study design and location. For

example, the studies cited occurred in clearcuts, rather than understory settings. Herbaceous vegetation was only impacted as part of the site preparation treatments; in my study I deliberately controlled herbaceous vegetation in the annual weeding treatment.

The role and impact of deer and rabbit herbivory in this study was evident after removal of the protective mesh cages after the third growing season. I observed browse damage on most seedlings once exposed, which is typical throughout much Minnesota (Sauerman 1992, Davis *et al.* 1998, Saunders and Puettmann 1999b). The actual intensity of browsing numbers may be artificially inflated as I may have created conditions that concentrated browsing by clearing experimental plots and planting in the midst of vigorous woody regeneration and shrubs. Saunders and Puettmann (1999b) suggest that removal of competing vegetation resulted in decreased hiding cover, exposing seedlings to an increased probability of browsing.

During my five-year study, blister rust was not a major source of mortality even though this site is located in a high-risk zone (Zone 4) for the disease (Brown *et al.* 1999). The mortality rate of approximately 12% is consistent with those recently reported for pole and small timber size white pine in northern Wisconsin of 7.2% to 15.9% across a range of high risk sites by (Dahir and Cummings Carlson 2001). Actual infection rates in my study are likely underestimated, as blister rust infections are not likely to be detectable for a few years after the disease enters the tree (Hunt 1997). In general, as the seedling cover (both overstory und understory vegetation) was reduced, the probability of blister rust infections increased. This is likely due to microclimatic conditions favorable for blister rust infection as predicted by Van Arsdel (1972) and Gross (1985). Anecdotal evidence indicates that rabbits prefer to browse on stem cankers, and the possibility exists that this herbivory may have removed part of the infected plants in the plots.

Pine bark adelgids were present across the entire site. As with weevil attacks, adelgids rarely cause seedling mortality in Minnesota, but may slow growth or affect seedling vigor (J. Krueger personal observation, unpublished data). Results indicate that adelgids, like weevils, may be found more often on faster growing trees that occur in relatively open growing conditions. White pine weevil also appeared to be of little

importance at this site. Although weevil attack is not typically associated with seedling mortality, weevils reduce height growth by killing terminal leaders. Due to the small number of trees affected I cannot conclude that weevil attacks occurred more frequently on plots that were more open, the condition typically associated with increased incidence of weevil attack. My visual analysis seems to agree with Stiell and Berry (1985) and Pubanz *et al.* (1999), who indicated that denser canopy cover typically resulted in small seedling terminal diameters, which do not favor weevil infestation (Katovich and Morse 1992).

Conclusion

This study illustrates the complex interaction between factors and responses that need to be considered when manipulating residual stand structures and species composition after harvests. Opening up overstory canopies to improve growing conditions for seedlings resulted in increased height and diameter growth of underplanted seedlings. On the other hand, benefits of weeding treatments were consistent for height growth, but limited to areas with relatively open overstory conditions for diameter growth. This supports the recommendation by Smidt and Puettmann (1998) that green tree retention or shelterwood treatments can be effectively used to control understory competition. This seems especially important on mesic hardwood sites, where more vigorous understory vegetation can be expected. Particular attention should be paid to treating dense hardwood regeneration and shrubs to reduce competition for light, soil moisture and nutrients. On this site, removing herbaceous vegetation provided little benefit.

Silvicultural operations aimed at creating favorable growing conditions for seedlings may also have drawbacks. White pine seedlings growing in more open conditions are generally more susceptible to herbivory, white pine blister rust, white pine weevil, and pine bark adelgid infestations. Thus, for any site a balance must be struck between conditions that favor growth rates and risking higher incidences of injuries and mortality. The incidence of damage agents does not imply the failure of a silvicultural treatment. For example in this study the insect and disease incidence rates were not significant causes of mortality. The ultimate importance of any damage agent is not the

influence on individual seedlings, but rather the combined impact that insects, disease, and herbivory have on the recruitment process and seedling to stand stocking levels.

Acknowledgement

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Table 2.1 Soil nutrient analysis of the study site.

Depth	pH	Bray-P	K	Ca	Mg	Na	NO-3-N
0-15 cm	5.6	10	77	1314	142	32	2
16-30 cm	5.8	6	51	947	94	35	0.6

Table 2.2 Results of the ANCOVA investigating the influence of canopy density and weeding treatment on total height and basal diameter four years after planting.

Source	Coefficient	df	MS	F	Pr > F
Mean Height Yr 4					
Model		3	13402	31.24	<0.0001
BA	-2.3	1	18903	44.06	<0.0001
WEED		2	10496	24.46	<0.0001
Error		133	429		
WEED-Annual	-2.76				
WEED-Monthly	0				
WEED-Control	-27.63				
Mean Diameter Yr 4					
BA	-0.53	1	551	54.09	<0.0001
WEED		2	287	28.15	<0.0001
BA*WEED		2	57	5.59	0.0047
Error		131	10		
WEED-Annual	-1.21				
WEED-Monthly	0				
WEED-Control	-11				
BA*WEED-A	0.1				
BA*WEED-M	0				
BA*WEED-C	0.38				

Table 2.3 Regression results and coefficient estimates quantifying the influence of initial height, herbaceous cover, shrub cover, and DIFN on height and diameter growth in years two and four.

Source	Coefficient	df	MS	F	Pr > F
Height Growth (yr 2)					
Model		4	276	43.89	<0.0001
Initial Height	0.22	1	84	13.32	0.0004
Herb Cover	-0.02	1	16	2.6	0.1094
Shrub Cover	-0.04	1	174	27.67	<0.0001
DIFN	11.4	1	681	108.43	<0.0001
Error		139	6		
Height Growth (yr 4)					
Model		5	1255	38.43	<0.0001
Initial Height	0.58	1	1129	34.6	<0.0001
Herb Cover	-0.01	1	5	0.15	0.7034
Shrub Cover	-0.1	1	439	13.45	0.0004
DIFN	23.12	1	123	3.77	0.0554
Initial height*DIFN	-0.33	1	107	3.27	0.0737
Error		90	33		
Diameter Growth (yr 4)					
Model		6	40	33.81	<0.0001
Initial Diam	0.57	1	20	16.54	0.0001
Herb Cover	-0.01	1	2	1.28	0.2617
Shrub Cover	0.01	1	0.5	0.38	0.5398
DIFN	11.21	1	17	14.16	0.0003
Initial Diam*DIFN	-0.67	90	9	7.82	0.0063
Shrub Cover*DIFN	-0.08		13	10.67	0.0015
Error		90	1		
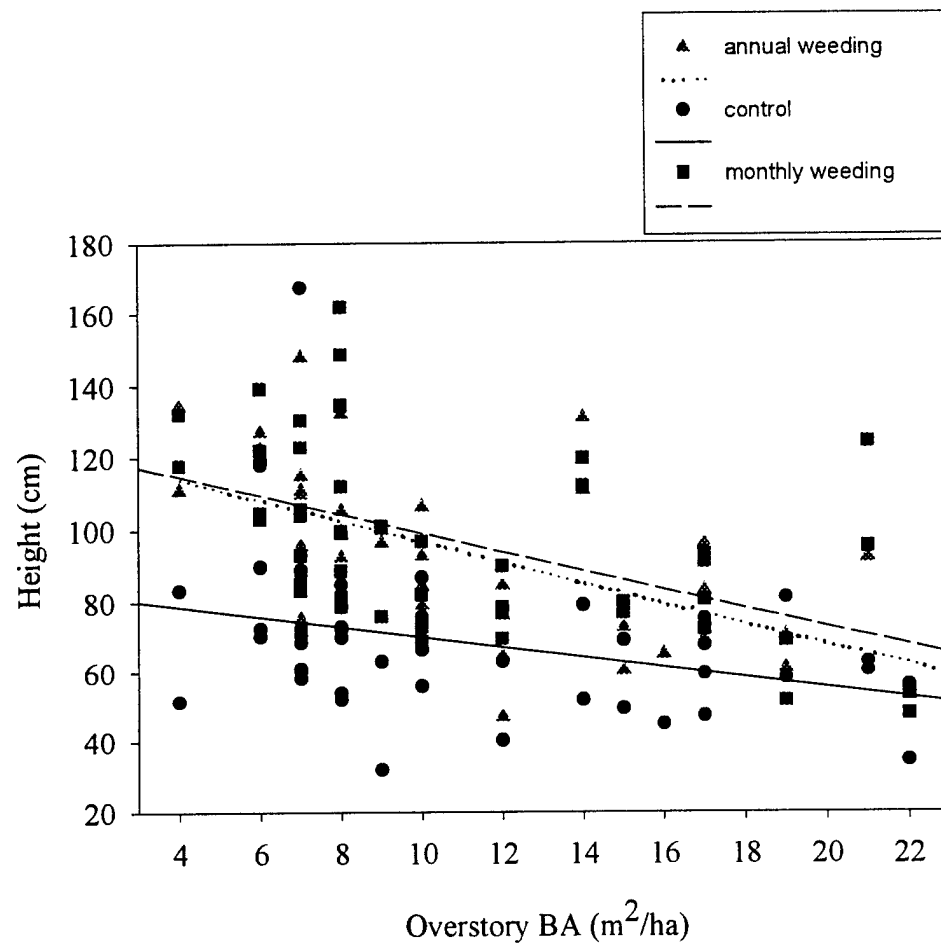
Figure 2.1a Height after 4 growing seasons as influenced by overstory basal area and weeding treatments.
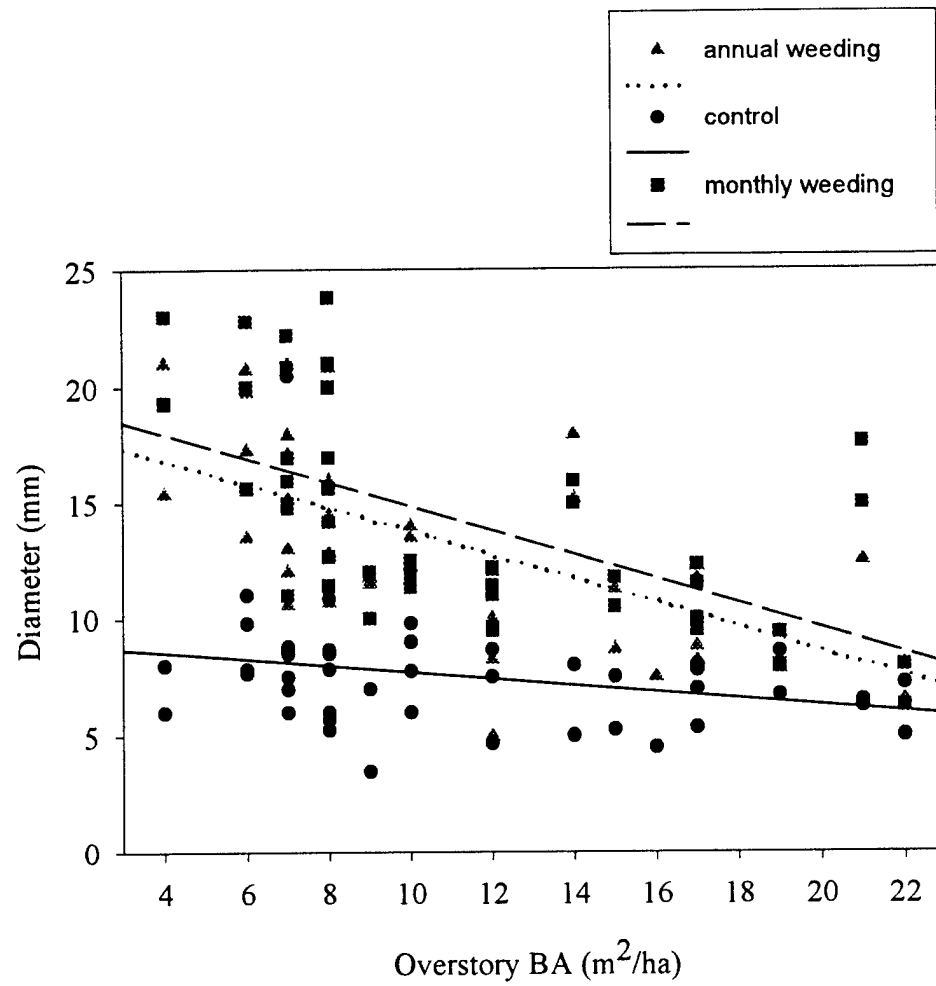
Figure 2.1b Basal diameter after 4 growing seasons as influenced by overstory basal area and weeding treatments.
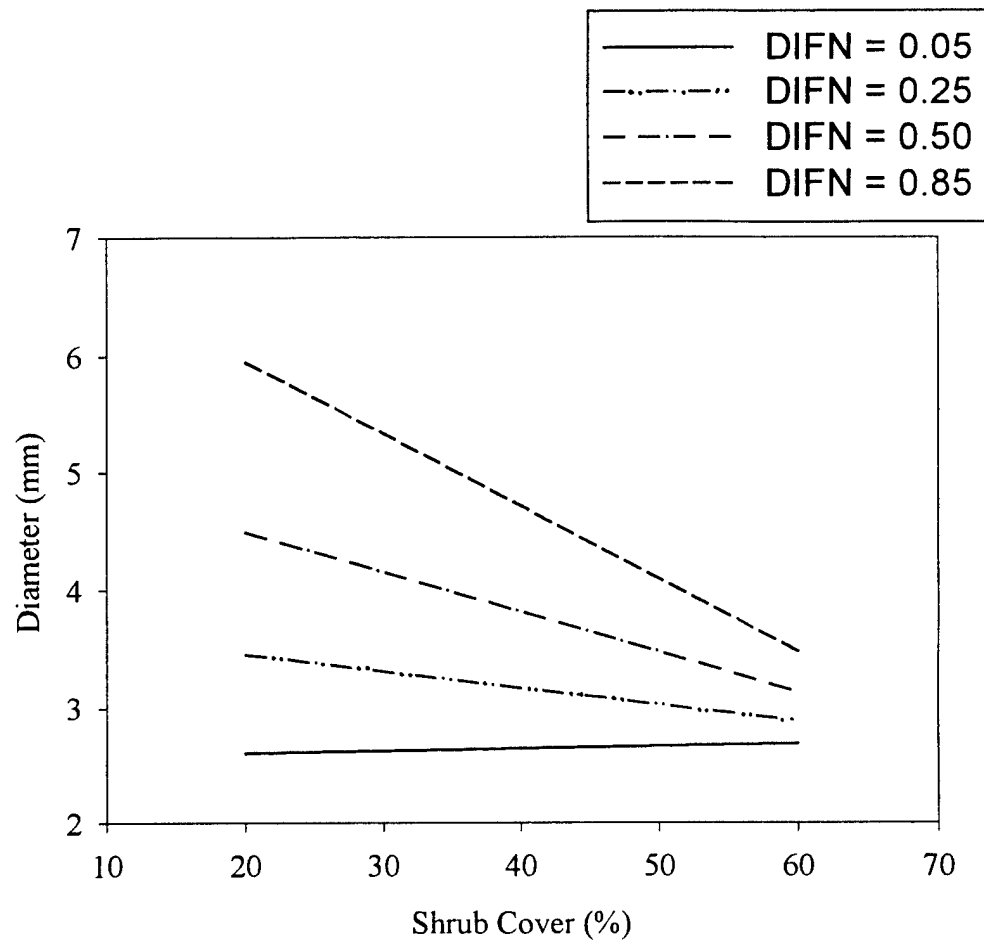
Figure 2.2 Basal diameter growth in year four as influenced by shrub cover and DIFN.
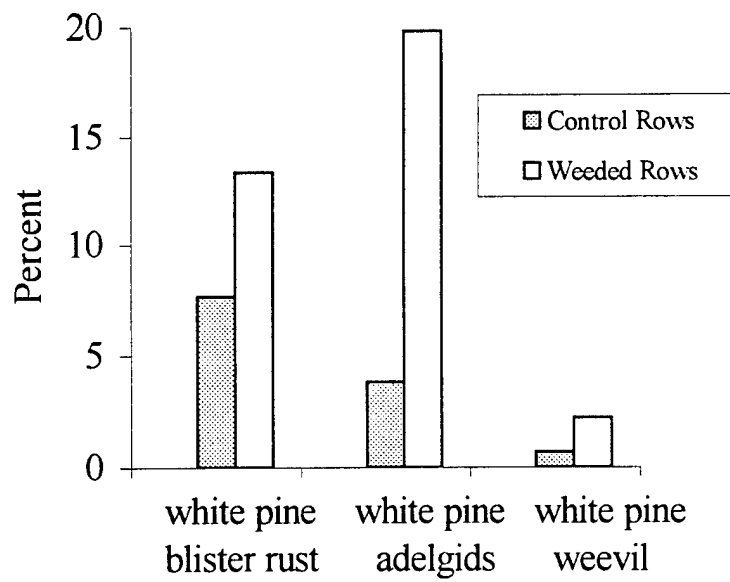
Figure 2.3 Percentages of seedlings in weeded and unweeded rows that were affected by white pine blister rust, white pine adelgid and white pine weevils.

CHAPTER 3

Modeling the regeneration dynamics of

eastern white pine (*Pinus strobus* L.)

Format is for Journal of Applied Ecology

Summary

1. First year recruitment and second year growth and survival for eastern white pine were modeled for naturally regenerating stands in northern Minnesota. Variable estimation modeling techniques were combined with regression analysis to construct three stochastic sub-models that define the regeneration process.

2. The model predicts germinant recruitment within stated site conditions in a single year time step. Results indicate that white pine may be seed and safe site limited. Germinant densities are most sensitive to seed availability, safe site availability, stand structure, and mortality functions. Growth is most sensitive to initial height, overstory canopy closure, and competition from woody understory vegetation.

3. Results confirm a well known principle of regeneration silviculture that germinant populations are highly variable and subject to influences of site factors and numerous random processes.

4. The model can be parameterized to model silvicultural applications for evaluating the influence management actions have on ecological processes and assist in risk avoidance in regeneration planning.

Introduction and background

Understanding the relationship between the diverse set of ecological factors influential in the recruitment process is a central focus of research into regeneration dynamics. Ecological factors that influence natural regeneration are complex and modeling techniques are required to explore how these factors interact in facilitating or inhibiting the regeneration process. This study describes the development of a process based regeneration model designed to examine the interaction of factors deemed crucial to recruitment. My model represents a tool designed to capture the best available information on individual factors and test their interaction in predicting short-term germinant densities, survival, and growth. To illustrate the application of this process I have elected to examine the regeneration dynamics for eastern white pine (*Pinus strobus* L.) in northern Minnesota.

Individual elements of the regeneration process are well understood and many good conceptual models have been developed that identify individual components and their role in the regeneration process (Bormann & Likens 1979, Barnett & Baker 1991, Zasada *et al.* 1992, Grime 2001). In the transition from conceptual to empirical modeling, researchers have examined many of the individual components of the recruitment process, but are only beginning to build more complex, empirical-based regeneration models (Nyland 1997). Process based models (PBM) are widely applied in natural resource applications such as constructing fire management programs, predicting regeneration in grassland communities as well as predicting small mammal population dynamics (Grime 2001, McCarthy, Possingham & Gill 2001). In an attempt to develop a PBM of the recruitment process in boreal forests, 5 broad-based biotic recruitment parameters (basal area, seed mass, asexual production capacity, dormant seed bank capacity, shade tolerance) were identified and attempts made to establish deterministic relationships between factors (Greene *et al.* 1999). The authors concluded that although key recruitment processes were identified and validated, there was insufficient knowledge available to develop a plausible multi-species landscape level simulator.

As PBM's have become more common, model frameworks have evolved to include stochastic elements (Robinson 1998). Including stochastic elements that reflect biological variations for model components provides a means to increase the capacity of

regeneration models to predict recruitment patterns at the stand level in a realistic manner over a range of conditions and scales (Ek 1982). In an example, stochastic modeling techniques were used to construct a species-specific regeneration model using 4 site conditions (slope and azimuth, growth district and vegetation type, crown density, and quadratic mean diameter) to predict the occurrence, density and height for Norway spruce (*Picea abies* L.) in the forests of Austria (Schweiger & Sterba 1997). The authors concluded that the model behaved logically and in accordance with the silvicultural understanding of the species while yielding plausible predictions for recruitment. Ongoing research and development of PBM's have resulted in models typically restricted to examining a small number of factors for which a high degree of confidence exists to predict regeneration outcomes. While parsimony is a primary tenet for model construction, such techniques offer limited insight into the relationship among the model variables and model output.

I propose an extension to the PBM technique in which the model becomes a tool used to examine the influence and relationship between factors and the subsequent impact on germinant densities, early growth and survival. By describing and quantifying a broad range of factors influential to the regeneration process, we gain insight into the relationships that drive regeneration outcomes for an individual species. This represents a unique approach to utilizing the PBM method for regeneration studies. Model construction is accomplished by integrating variable estimation modeling techniques with regression and stochastic modeling processes. A strength of this technique is the capacity to build models to evaluate areas of interest in the absence of extensive experimental field trials or by using incomplete data sets. An overarching premise for this study is that it is reasonable and defensible to combine information on disparate ecological elements from multiple sources in a single model framework for predictive purposes. This study represents a unique application of regeneration modeling techniques by parameterizing numerous factors of the conceptual recruitment process to predict germinant density, early growth, and survival and analyze the relationship between model parameters (Tester, Starfield & Frelich (1997), Mäkelä *et al.* 2000). The objectives for developing this research approach are threefold:

- To gain insight into the regeneration process by investigating influential factors that interact to influence regeneration outcomes for an individual species.

- To obtain a biologically cogent regeneration process model to act as a multifactoral response surface to evaluate the influence of individual parameters and combinations of parameters on model output. A sensitivity and model application test are conducted.

- To predict regeneration outcomes (germinants/unit area and/or population height characteristics) under various stand conditions.

Characteristics of eastern white pine

White pine is a predominantly temperate, long-lived species that covers an extensive range extending from southeastern Manitoba, east to Labrador and south along the Appalachian Mountains to northeastern Georgia. The species is moderately shade tolerant, which permits establishment and survival in the understory. Germination is optimized on seedbeds composed of mixed mineral soil and organic matter, but is possible on diverse seedbed conditions. Although white pine grows on a wide range of soil conditions, it competes best on well-drained soils, which generally support less vigorous hardwood vegetation. In the western Lake States and Ontario, historical harvest operations combined with changes in land use and disturbance patterns have resulted in changes to the landscape that do not favor the natural establishment of white pine (Stine and Baughman 1992, Kershaw 1993). For additional information I refer the reader to Stiell (1978), Wendel *et al.* (1983) and Wendel & Smith (1990).

Methods

Model formulation

This model was developed to simulate the recruitment and growth for white pine germinants in northern Minnesota following disturbance to the existing forest canopy. Disturbance to the canopy is associated with the creation of safe sites in the understory suitable for white pine germination and early establishment. It is a species-specific, individual tree, gap resolution model that incorporates ecological interactions (Robinson 1998). The resolution is a 10 m X 10 m plot level (100 m^2) and by aggregating results, the model predicts regeneration outcomes at the stand level (per hectare basis). The

framework is hierarchical with sub-models linked and describes the relationships and influences of variables. The model is implemented on a MS Excel spreadsheet (Microsoft Corp.). As a verification of the sub-models I compared model results with results of experiments reported in the literature and unpublished data sets.

The model consists of three sub-models: recruitment, height growth, and mortality (Figures 3.1a, 3.1b, and 3.1c). The recruitment sub-model predicts germinant establishment in the first year; while the growth and mortality sub-models operate in the second year to predict height and survival. Predictions for population parameters are obtained by operating the model in either a deterministic or stochastic fashion under a given set of stand conditions. When the model is operated stochastically, population estimates are obtained by allowing variables to operate stochastically within specified bounds through repeated iterations. The model is calibrated for white pine regeneration, which results from either human induced or natural disturbance of the forest canopy and the subsequent creation of safe sites. The model is not used to predict regeneration outcomes for clearcut harvest operations or in stands where no disturbance has occurred. The current version of the model is limited to modeling two one-year time steps.

<u>Variables</u>

The variable set for each sub-model has been selected with the intent of capturing key information related to ecological conditions in a stand. Variables are divided into three categories: input, categorical, and output. A description of the variables, parameterization, sources and assumptions is located at Appendix 1. The first two chapters of my thesis provide additional information on the relative influence and interaction of a selection of these variables.

The value for input variables are determined by the user to define specific stand-level conditions. Inputs define a stated condition for a forest stand and represent either known population distributions or estimated ranges of conditions. Values input by the user are manipulated, provide interim output and are used sequentially as input for the next step in the modeling process. Categorical variables represent specific stand attributes that modify model processes. For example, if the category bumper seed crop is selected, a specific range of seed production is then determined. Output variables

represent predicted population characteristics such as germinant density and height distributions.

Parameterization

Means, distributions, and ranges are derived from the literature, direct observations, experiments, and unpublished data sets. The recruitment and mortality sub-models are parameterized using a range of sources to establish or adjust variable values and model fitting procedures (Pastor and Post 1985, Sievänen and Burk 1993). To parameterize the model for the sensitivity test, low and high values for each factor are assigned based on information obtained in the literature, direct observations and experimentation. To conduct the model application test, stochastic processes associated with individual factors are modeled using a range of stated conditions with a postulated normal distribution and mean. The exception is the variable seed year generator (SYG), which has a uniform distribution. The growth sub-model uses an equation developed from results of white pine underplanting experiments conducted in northern Minnesota.

Uncertainty and variation

Uncertainty is inherent in each variable and is a function of the quality of its source and method of utilization. In addition, uncertainty arises from concerns about the validity of the model structure used to describe the regeneration process (Robinson & Ek 2000). To minimize uncertainty, population distributions obtained from unpublished data are incorporated when available. The majority of variable parameterization is gleaned from the literature. As a result, no specific measure of the error budget is possible for the overall model. To minimize error the model is tested and applied under constraints where disturbance has occurred and a partial canopy remains. Appendix 1 addresses the assumptions that influence uncertainty and variation associated with individual variables.

Recruitment sub-model

The recruitment sub-model (Figure 3.1a.) characterizes the integration of several biotic and abiotic factors described in Chapter 1 of this thesis. The model provides a quantitative approach to describing, testing, and predicting the influence of these factors on the recruitment of white pine in a single year. In the context of this study recruitment describes the interaction of factors that result in the germination of white pine seeds and

first year survival of seedlings. The parameterization for this sub-model is accomplished exclusively from the literature and unpublished data sets.

The recruitment sub-model is composed of a series of factors that follow the biological sequence for regeneration. The structure of the sub-model is frame-based (Starfield *et al.* 1993). In the frame based approach used in this study, each factor represents a specific process, which defines an individual frame of the model [1]. Within the sub-model the recruitment process begins with seed production and terminates at the close of that first year of establishment. This represents the first of the two one-year time steps modeled. The recruitment sub-model is composed of factors that represent a range of unique equations, proportions, or distributions that combine to predict germinant density.

The following describes how factors are calculated and relate mathematically in the sensitivity test. To conduct a 2^k factorial sensitivity test each factor is assigned a constant low or high value. Parameter values used to conduct the test are reported in Table 3.2. The equation used in this test is:

[1] $$GT = SP * SV * SD * (1-PD) * SS * (1-IM)$$

The initial frame represents the density of white pine seed trees in m^2/ha. White pine basal area (WPBA) is used as an input in the determination of white pine seed production/ha. The sensitivity test is conducted for three values of WPBA: 10 m^2/ha, 28 m^2/ha, and 43 m^2/ha. Seed production (SP) is a factor that represents the quantity of white pine seed produced on a per hectare basis for a given value of WPBA. The following method was used to develop values for seed production used in the sensitivity test. Seed production on an area basis as a function of seed tree density is interpolated from a smoothed line of a plot of observed seed production values. The smoothed line was constructed by calculating a mean seed production value per unit of seed tree basal area reported for two years of reported seed production in an 80 year old even-aged white pine stand (Graber 1970). I calculated the high and low value for seed production as ± 25 % of the mean seed production. To maintain the plot level scale for the model the seed production per hectare value is reduced to a plot basis by multiplying by 0.01.

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The remaining set of factors in the sub-model act as ecological sieves that sequentially reduce the biological potential for regeneration represented by white pine seed production. Seed viability (SV) represents the proportion of seeds produced that will germinate and have the potential to develop into seedlings. In the sensitivity test seed viability is a constant set to 0.8. The value for viable seed produced is calculated by multiplying SP by SV.

The next variable is seed distribution (SD), which predicts the proportion of viable seed produced (SP*SV) that will land a given distance from the seed source. Two equations were developed to predict differential seed distribution between inside a stand [2] and outside a stand [3].

[2]   proportion seed deposited (SD) = EXP (4.605-0.05 * DP)

[3]   proportion seed deposited (SD) = EXP (4.605-0.014 * DP)

The equations were developed using a linear transformation of a negative exponential decay function commonly associated with wind disseminated seeds (Okubo & Levin 1989, Keen & Spain 1992). As used in this study, SD is related to residual stand structure following the partial disturbance. The inside stand SD equation predicts the dissemination of seeds in a stand that is relatively intact, while the outside stand SD equation predicts seed dissemination in a stand that is relatively open. To model the decay rate of seed deposition associated with distance from the seed source I assume 100 % of seed is available at the seed source and it diminishes to 5 % at the maximum dispersal distances of 60 m within a stand and 210 m outside a stand (Okubo & Levin 1989). The linear relationship between seed deposition and distance was used to develop the two linear regression based seed dissemination equations [2 and 3] (SAS V. 8.2, SAS Institute Cary, NC). For sensitivity testing the distance value in the equation is derived from the specified high and low values. The proportion of seed deposited (SD) determined in the equation is multiplied by the viable seed produced (SV*SP) to arrive at the quantity of viable seed.

The next parameter is an estimation of seed predation (PD) expressed as a proportion of the seeds that are consumed or removed. The proportion of seed remaining

following predation (1-PD) is multiplied by the value for viable seed to determine the post-predation seeds. The next parameter safe site (SS) calculates the number of post predation seeds that have landed on a safe site. Safe site represents the proportion of the plot that can support germination and early establishment. The value for safe site is multiplied by the value for post-predation seeds to determine the quantity of initial germinants (IG).

The number of initial germinants (IG) is then reduced by the initial mortality parameter (IM). Mortality is expressed as a proportion of the germinant population that will die by the end of the first growing season. The value determined for germinants that survive initial mortality (1-IM) is multiplied by the value for initial germinants (IG) to determine the end of season germinants (GT). To obtain estimates at the per hectare scale the GT value on the per/plot basis is multiplied by 100.

Height growth sub-model

To determine the influence of cover type and competition on the height growth of germinant white pine I have developed a growth sub-model. The sub-model operates at the individual tree level in a one year time step in the year following seedling germination and establishment. The sub-model consists of 4 factors and one interaction (Table 3.1, Figure 3.1b). The data used to construct the height growth equations were derived from a series of experiments that used planted white pine seedlings (3-year old nursery stock) in sites located in northern Minnesota. The results of one of these experiments is described in Chapter 2 of my thesis. Data on 3 cover types (conifer, northern hardwoods, and oak-maple) were obtained from the white pine database and evaluated. The regression analysis was accomplished for each cover type and values for the coefficients derived from the regression equations are given in Table 3.4.

The analysis was restricted to conditions represented in the data set used for model construction. The height of the germinant at the end of the growing season (ESH) is a function of its initial height and the overall competitive environment [4]. The factors initial height of the seedling (IH), overstory canopy closure (OCC), understory competition (UC), percent herbaceous vegetation cover (HB) and the interaction between the overstory and understory (OCC X UC) were selected and are used to model individual tree height growth.

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[4] $ESH = \beta_0 + \beta_1\,IH + \beta_2\,OCC + \beta_3\,UC + \beta_4\,HB + \beta_5\,OCC \times UC$

Construction of the three cover type growth equations was accomplished using the multiple linear regression technique (SAS V. 8.2, SAS Institute, Cary NC). Statistical significance was considered in variable inclusion in the growth equation. However, factors were not automatically rejected based on a specific p-value or threshold. Instead, statistical significance was used as a guide with the intent to create equations that contained the same variable set. In the model fitting process factors that were clearly not significant across all three cover types were rejected. The construction of each cover type equation was restricted to the same information from each data set in order to isolate the unique influence of factors by cover type on seedling growth. In an attempt to minimize error propagation associated with planted stock, the equation development is limited to using data from the first year following planting. Coefficient values for each variable are listed in Table 3.4 with a summary description for each cover type in Appendix 2.

The following describes how factors relate mathematically in the sensitivity test of the growth sub-model. To conduct the 2^k factorial sensitivity test the individual factors are assigned constant low or high values. These values are reported in Table 3.4. To determine the values for individual factors a series of scatter plots were constructed from the white pine database. In each scatter plot the value for year two seedling height was plotted as the y-axis value over the x-axis values for initial height (IH), overstory canopy closure (OCC), and herbaceous cover (HB). This was accomplished for data for each cover type. Values for the high and low parameter settings were selected based on representative values from each scatter plot and cover type. The intent was to test like values for each cover type by capturing the range of conditions representative of the observed data.

Once a cover type equation is selected for testing, the value for end of season height (ESH) is derived in the following manner. The value for the intercept (β_0) is added to the individual products obtained by multiplying the coefficient values by either

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the low or high parameter value. The sum represents the cumulative height in centimeters of an individual tree at the end of the growing season.

Mortality sub-model

The mortality sub-model is designed to capture the influence of a broad range of mortality agents on germinant population structure. The sub-model contains 3 factors: winter mortality (WM), spring herbivory (SH), and summer mortality (SM) which all act to reduce the second year germinant density (SG). The sub-model operates in the year following germination and establishment (Table 3.1, Figure 3.1c, Appendix 1). The output from this sub-model is the predicted germinant density per plot (X100 = per hectare) at the end of the second year (EG). The equation is:

[5] $$EG = SG * (1 - WM) * (1 - SH) * (1 - SM)$$

Germinant survival (EG) is a result of the cumulative reduction from broad-based mortality functions that include winter mortality (WM), spring herbivory (SH), and summer mortality (SM). Each mortality factor represents a proportion of the population that dies and reduces the germinant density. The sub-model is parameterized based on the predicted variation in mortality agents as a function of disturbance and associated changes to environmental conditions on the forest floor (Appendix 1). Investigating mortality patterns and the influence on germinant populations provides clues to the short-term dynamics observed in germinant populations. A limitation of modeling mortality functions collectively is that only broad inferences can be made about the influence of collective mortality factors.

Sensitivity Testing

Sensitivity analysis was conducted to test the relationships between parameters in the recruitment and growth sub-models under hypothetical stand conditions. In this test each sub-model is configured to operate in a deterministic manner. To conduct the test each factor is assigned a discrete value, modeled, and the output (i.e. first year germinant density or end of season height) is evaluated. As individual factors are assigned discrete values for the test they act as parameters within the model. By evaluating model output as a function of the unique combinations of the sets of parameters, a determination can be

made about the sensitivity of the model to changes in the value of single or combinations of parameters. Examining the relationships among parameters provides potential explanations for observed short-term regeneration patterns at the stand level and may provide insight into recruitment patterns that occur at the landscape level.

A full factorial sensitivity test was conducted for the recruitment and growth sub-models by utilizing a 2^k factorial test procedure (Jain 1991). The high and low values assigned to each parameter are representative of conditions reported or observed for white pine seedlings (Appendix 1). The recruitment sub-model test uses a 2^6 design replicated for three levels of seed tree density and two levels of seed distribution equations. The result is a 2^6 X 3 X 2 design for a total of 384 permutations of the sub-model. The height growth sub-model is tested using a 2^4 design with 3 levels of cover type, which results in a 2^4 X 3 design for a total of 48 permutations for the growth sub-model.

I tested the following parameters from the recruitment sub-model: seed production (SP), seed viability (SV), distance to plot (DP), seed predation (PD), safe site (SS), and initial mortality (IM) (for values see Table 3.2). The parameters were tested in combination with 3 levels of seed tree density 10 m^2/ha, 28 $m^{2/}$ha, and 43 $m^{2/}$ha, hereafter referred to as low, medium and high density. In addition each test was replicated using the inside stand and outside stand seed distribution equations. In the growth model I tested the following factors: initial height (IH), overstory canopy closure (OCC), understory competition (UC), and herbaceous cover (HB), in conjunction with coefficients for the 3 cover types (Table 3.4). As the experiment is designed in a factorial manner it is appropriate to use a factorial analysis of variance (ANOVA) to evaluate the output. To analyze the results of the sensitivity test I conducted a factorial ANOVA using the general linear model (GLM) procedure (SAS V. 8.2, SAS Institute, Cary, NC). It is important to note that changing the range of values tested (high, low) for each parameter would result in changes to the influence each has on germinant density or height (GT, ESH) and the statistical significance of that parameter.

I did not conduct sensitivity testing on the mortality sub-model. This is due to the limited reliability of the range of mortality estimates modeled and the negative, linear relationship between the factors and germinant density. As each mortality factor

functions as an ecological sieve removing a proportion of germinants, any increase in each of the mortality rates results in an equal reduction in germinant population.

Sensitivity Test Results

Results of the sensitivity test indicate that germinant density at the end of the first year (GT) is most sensitive to seed availability, initial mortality rate, and safe site availability (Table 3.5a, Figures 3.2a, 3.2b, 3.2c). Seed availability as a function of distance to plot (DP), seed distribution equation (SD), and seed production (SP) account for 43 % of the variability in predicting first year germinant density (GT) (Table 3.5a). The most influential individual parameter is distance to plot (DP), which represents the proximity of the plot to the seed source, and accounts for 27% of the variance. The range of predicted germinant density as a function of seed tree density was from 100 to 373,000/ha at 10 m^2/ha, 300 to 905,000/ha at 28 m^2/ha, and 200 to 533,000/ha at 43 m^2/ha. In general, recruitment levels are highest at medium levels of seed tree density and when seeds are disseminated using the outside of stand equation. Equivalent results of approximately 25,000 germinants/ha are obtained when low or high seed tree density are modeled using high seed production rates and the medium density stand is set to a low seed production rate. The lowest recruitment rates of 300 germinants/ha or less result only when sub-optimal conditions exist for each parameter regardless of seed tree density levels.

Verification

The recruitment model appears to perform well as seedling densities from model applications seem to match densities found in a number of field studies. Maximum seed planting rates for white pine of 370 seeds/m^2 (3,700,000/ha) are recommended in nurseries (Krugman & Jenkinson 1989). In specific field trials, mean germinant densities of up to $\approx$ 250,000 germinants/ha are reported two years following site preparation treatments in a white/red pine shelterwood study (Burgess, Wetzel & Baldcock 2000). When follow-on mortality is considered, the range of recruitment predicted by the model falls within the very broad ranges reported for naturally regenerated stands resulting from partial canopy disturbance in temperate white pine forests (Baldwin 1940 and 1957, Burgess *et al.* 2000). High levels of recruitment coincide with high levels of seed

production tied to optimal stand conditions while low levels result from periods of low seed production and sub-optimal combinations of the other factors.

When high levels of safe site (SS = 75 %) are combined with high seed production rates and optimal combinations of remaining factors, germinant densities typically exceed 500,000/ha at the medium seed tree density level where seed production peaks (Appendix 1). Conversely, for medium seed tree density stands when high seed production rates are combined with low safe site levels (SS = 20 %), germinant production is reduced by nearly 90 % to 53,000/ha (SD = inside stand seed). Similar trends related to germinant density levels are obtained when comparing results for the high and low seed tree density levels (Figure 3.2c).

Height growth of germinants is most sensitive to initial height and overstory canopy closure. Initial height is clearly the single most influential factor accounting for 95% of the variation in predictions for end of season height (ESH) (Table 3.5b). The influence of initial height is an important component for growth projection, with each additional centimeter of height resulting in a predicted growth of 1.1 cm for the oak-maple cover type to 1.2 cm for the conifer and northern hardwoods cover types. Overstory canopy closure is the next most influential factor and accounts for 3% of the variation in end of season height (ESH, Table 3.5b). The largest values for height growth occur when overstory canopy closure levels are low and competition from understory woody vegetation is absent (OCC = 0.3 and UC = 0). Using comparable settings for each cover type, the largest single year growth increment is associated with the oak-maple cover type at 8.4 cm and the northern hardwoods cover type at 8.3 cm. A much lower single year growth increment of 3.5 cm results from the conifer cover type (UC= 0, HB = 0 to isolate overstory influence). In analyzing the influence of competition from understory woody vegetation on germinant height growth the greatest negative influence is observed under the conifer and oak-maple cover types with cumulative heights 25.1 cm and 24.9 cm respectively and the least influence in the northern hardwoods cover type with a predicted height of 28.2 cm (IH = 10 cm, OCC = 0.3, HB = 0). The influence of herbaceous cover on growth produces mixed results (+/- coefficient values) among the different cover types. As discussed in Chapter 2 of this thesis, competition from

herbaceous vegetation in shelterwood conditions tested generally has very little practical impact on height growth (Table 3.4).

Verification

Specific growth patterns for tree germinants in temperate forests are a relatively unexplored and unreported area of investigation. This represents a limitation to verifying the growth sub-routine. Cornett (1996) and Smith (1940) reported cumulative germinant heights for the second and third years, without reporting incremental growth. A verification of height growth output was accomplished by comparing the regional white pine germinant height data reported by Cornett (1996) to similar model results. The conifer cover type growth equation was utilized by postulating values for variables representing stand conditions described by Cornett and operating the growth routine through a two year time step to obtain results. Results from the sub-model prediction of growth exceed those observed by Cornett (1996) by greater than 1 standard deviation. I conducted an additional verification for the conifer and northern hardwoods cover type growth sub-routines. A further verification was accomplished using unpublished data sets from additional planted white pine studies located in Itasca County, MN that were not included in the development of the growth sub-routine regression. An examination of the regression coefficient values for the conifer and northern hardwoods cover types indicate similar results would be obtained from using these data.

Model application test: testing 3 silviculture scenarios

This test represents an application and evaluation of the model that incorporates stochastic processes associated with variables in each of the sub-models. This test is designed to evaluate variable interaction and the capacity to model the probability of regeneration outcomes. The intent is to evaluate the importance of a set of stochastic ecological factors, as influenced by various management activities. The model application test uses conditions characteristic of stand manipulation practices common in regeneration silviculture operations for white pine in northern Minnesota. In this test each sub-model operates in a stochastic manner based on a probability-tree process model (Ek 1982, Keen & Spain 1992).

Three scenarios are constructed by parameterizing the model to reflect a range of stand conditions associated with specific management activities (Table 3.6). In this series

of tests a silvicultural scenario represents a set of activities categorized as a shelterwood (low density = 9 m²/ha and high density = 19 m²/ha) or seed tree method (5 m²/ha). The shelterwood and seed tree method represent commonly applied forest regeneration techniques where varying amounts of the forest canopy are retained following a partial harvest (Hannah 1998, Nyland 2002). Residual canopy trees represent an *in situ* seed source as well as a means by which fluctuations in soil moisture, surface temperature, and damage agents are mediated (Hannah 1998). The residual overstory canopy also competes for light, moisture, and nutrients, which influences seedling vigor, growth, and eventual survival (see Ch. 2). The model is parameterized for each scenario using values for variables specified in Table 3.6. To obtain estimates of a mean and standard deviation for each sub-model output (GT, ESH, and EG) the model is operated stochastically using a Monte Carlo technique (1000 iterations). The distribution of sub-model outputs is used to evaluate the three levels of management activities and the influence of tested variable interactions.

For the purposes of this test the overstory consists of an even-aged white pine cohort that has been harvested to 3 different levels of residual density (basal area). The residual trees are assumed to be healthy and vigorous. The management objective was to harvest a quantity of the overstory, yet retain sufficient residual density to provide a seed source for regeneration and shelter for germinants. During this hypothetical operation, consideration was given to routing equipment in a fashion that optimized mixture of the organic seedbed and mineral soils to enhance safe site creation targets. It is assumed that the modeled stands are subject to the same ecological influences not included in the model. Table 3.6 contains information on the specific values for each factor and the model output.

Within this test the values for the following variables differed between management scenarios: seed production (SP), safe site (SS), initial height (IH), overstory canopy closure (OCC), herbaceous cover (HB), and spring herbivory levels (SH) (Table 3.6). To test the influence of residual stand density, the inside stand seed distribution equation was used for to evaluate the shelterwood methods and the outside stand equation was used to test the seed tree method. In the low density shelterwood scenario, the understory competition index (UC) was set to 0 to reflect initial understory woody

vegetation control achieved via the harvest disturbance. In the seed tree scenario UC was also set to 0 to represent the absence of woody vegetation following the more extensive harvest operation. In the high density shelterwood UC was set to 1 to represent lower levels of harvesting disturbance to understory woody vegetation. Remaining variables were consistently applied to each scenario (Table 3.6). The equation for the conifer cover type was used to model height growth. I constructed a large-sample 95% confidence interval for the mean of each sub-model to evaluate differences in the population predictions as a function of the stand attributes tested. Variables are randomly determined within the model and assumed to be normally distributed. Variables are tested using a postulated mean and variation based on target or anticipated stand conditions following the harvest. In each case the mean is calculated as the mid-point of the postulated range and one standard deviation is calculated using the empirical application of Chebyshev's Rule for normally distributed values as 0.34 * hypothesized range.

The following process describes how the variables are calculated and relate mathematically in this test. Equation [1] is modified in the following manner for this test:

[1] $GT = SP * SV * SD * (1-PD) * SS * (1- IM)$

For the recruitment sub-model the initial frame establishes the density of white pine seed trees (WPBA) in m^2/ha (Figure 3.1a). As in the sensitivity test, the value for WPBA is used as a basis to determine the value for seed production. However, in this test seed production is modified by including the stochastic variable masting cycle. The next variable is the seed year generator (SYG) whose value determines the category for masting cycle (MC). The seed year generator is a uniformly distributed random number bounded by 1 and 100 (Appendix 1). The MC variable models the seed masting process known to occur in *Pinus* and is represented by four categories: failure, moderate, good, and bumper. The frequency of occurrence for each MC category is: failure 20%, moderate 50%, good 22%, and bumper 8%. Each MC category represents a normally distributed random variable that corresponds to a range of seed produced as a proportion of the maximum potential seed production per unit of seed tree density (Appendix 1). The range of seed production by MC category is: failure 0.1 % (low) to 3 % (high) of

maximum, moderate 4 % (low) to 25 % (high) of maximum, good 26 % (low) to 74 % (high) of maximum, and bumper 75 % (low) to 100 % (high) of maximum.

The following method was used to calculate seed production (SP). A hypothesized benchmark for a maximum seed production rate per unit of seed tree density is derived from the 1965 seed production data reported by Graber (1970)(Appendix 1). The seed production data for 1965 was plotted and a smoothed line applied. For each level of WPBA modeled, a specific value for seed production is interpolated from the smoothed plot. The value for SP derived from the plot corresponds to the hypothesized maximum seed production on a per hectare basis for the specified level of WPBA. The range of values for SP/ha used in the test is calculated by multiplying the low and high value established for the MC category by the maximum seed production value for the established seed tree density associated with the specific scenario being tested. The values derived for seed production in this process represent the potential range production for that year.

Seed viability (SV) is the next factor and represents a constant value of 0.8 for this test. Viable seed is obtained by multiplying the value for SP by 0.8. Distance to plot (DP) simulates a range of post-disturbance stand conditions where the distance in meters from seed source to plot varies. The variable is bounded at 0 and 100 m and the distance value generated is used as input for the seed distribution equation (SD).

The next variable is the seed distribution (SD) equation, which predicts the proportion of viable seed produced (SP*SV) that will land a given distance (DP) from the seed source. The two seed distribution equations [2] and [3] and the methodology are as described in the sensitivity test. The proportion of seed deposited is derived from the equation by multiplying the value for SD by the quantity of viable seed produced. The value determined represents the viable seed deposited.

The next variable is seed predation (PD) expressed as a proportion of the seeds that are consumed or removed. To calculate the quantity of seed remaining following predation, the proportion not predated (1-PD) is multiplied by the value for viable seed. The next parameter calculates the number of post predation seeds that have landed on a safe site (SS). The proportion safe site is multiplied by the value for post-predation seeds to determine the quantity of initial germinants (IG).

The number of initial germinants (IG) is then reduced by the initial mortality (IM). Initial mortality is expressed as a proportion of the seedling population that will die by the end of the first growing season. The proportion of germinants that survive initial mortality (1-IM) is multiplied times the value for initial germinants to determine the value for IG to arrive at the end of season germinants (GT). The value for GT is scaled to the per hectare basis by multiplying by 100.

The following describes the mathematical operation of the growth sub-model equation [4] as used in this test. The variable and coefficient values used in this test are presented in Table 3.6. Selection of the cover type and scenario determines the value and distribution for the intercept (β_0), regression equation coefficient values, and the initial height values (IH) (Table 3.6, Appendix 1). In this test the conifer cover type growth equation is used. The values for remaining variable distributions are determined based on estimated stand conditions that result from the harvest disturbance. The intercept (β_0) and the equation coefficients (β_1 to β_5) are allowed to vary stochastically within the operation of the test with a normal distribution (mean = coefficient value ± standard error). The value for the intercept (β_0) is added to the individual products obtained from multiplying the coefficient values by the values for each variable. The sum represents the cumulative height in centimeters of an individual tree at the end of the growing season.

Once the IH distribution is determined based on the scenario, it represents a normally distributed random variable. The next variable is overstory canopy closure (OCC) a measure of overstory resource competition. Understory competition is expressed as a conditional value (0 or 1) for modeling purposes. When the value for UC is set to 0 this variable and the value for the OCC X UC interaction becomes 0. The next variable is percent herbaceous cover in competition with seedlings. The final parameter is the OCC X UC interaction. The value for this variable is determined by multiplying the value of OCC by the value for UC and the interaction coefficient (β_5) ([6] in Appendix 1).

The following describes the mathematical operation of the mortality sub-model equation [5] as used in this test. The values for each mortality variable are presented in Table 3.6. The initial frame of this sub-model is the second year germinant population (SG) which represents a normally distributed random variable with the mean and

standard deviation derived from the germinant population (GT) generated in the recruitment sub-model. The end of season germinant population (EG) is derived by sequentially multiplying the value for SG by 1 – the proportion for each of the individual mortality functions (1-WM, 1-SH, and 1-SM) as specified in equation [5].

Application Test Results

The influence of the overstory density on germinant density is clear in each scenario tested. Increasing the seed tree density (in this test overstory density = seed tree density) from 9 m^2/ha to 19 m^2/ha resulted in increased the mean germinant densities by approximately 13,000 in the first year. When seed tree densities are low as in the seed tree method (5 m^2/ha), the resulting mean germinant density is approximately half that of the high density shelterwood (Table 3.6). An evaluation of the population means over the two year time step indicates that there is a trend toward congruency for the 5 m^2/ha and 9 m^2/ha populations while the 19 m^2/ha scenario germinant density is clearly larger than the other two (Figures 3.4a and 3.4b) High variation in germinant density at the lowest level of seed tree density (sd = ± 24,800 germinants/ha) results from longer seed distribution distances (DP). As observed in the sensitivity test, peak levels of variation in seed production and subsequent germinant densities are obtained when SP is highest at a seed tree density of 19 m^2/ha. In general, the high levels of variation in germinant densities obtained in this study are similar to observations from a regeneration experiment for white pine in which partial overstory removal yielded mean germinant densities of 0 to 243,000/ha 2.5 years following various harvest and site treatments (Burgess, Wetzel & Baldock 2000).

In each scenario the trends for first year germinants (GT), when grouped by germinant density category, are very similar (Figure 3.5). The probability of having 10,000 or fewer germinants/ha ranges from 31 % and 34 % for the high and low density shelterwood scenarios respectively to the highest probability of 45 % under the lowest overstory density conditions (Figure 3.5). The probability of obtaining greater than 20,000 germinants/ha occurs 31 % of the time for the seed tree method and greater than 55 % for the higher density shelterwood (Figure 3.5).

Differences in the residual overstory density and the absence of understory woody competitors did not appear to yield markedly different outcomes for height growth in

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shelterwood scenarios. At the end of the second year, mean heights as a function of canopy density were 19.6 cm (± 3.7) for the low density shelterwood and 18.1 cm (± 5.0) for the high density shelterwood. Height growth is greatest under the lowest canopy density (understory woody competitors absent) with a mean height of 27.2 cm (± 3.1). Congruence in height growth is indicated between the 9 m^2/ha and 19 m^2/ha shelterwood scenarios, with mean heights converging nearly within the 95% confidence interval and clearly within one standard deviation of each other (Table 3.6 and Figure 3.4b). The larger height growth associated with the seed tree scenario is a function of decreased influence from understory competition (UC = 0) and lower levels of competition from canopy trees.

The mortality sub-model investigated the influence of different spring herbivory rates on second season germinant density. The lower density shelterwood stand was subject to spring herbivory rates twice that of the higher density stand (50 % vs. 25 %) to represent a hypothesized increase in preferred browse created by the more extensive harvest. The difference in herbivory rate resulted in germinant densities of 10,800/ha (± 1,400) and 17,800/ha (± 15,100) respectively for the two shelterwood scenarios (mean ± sd). The high variation in germinant density for the high density shelterwood stand is a remnant of the first year population variation. The seed tree scenario used an herbivory rate of 38 % and resulted in germinant densities of 8,600/ha (± 10,100), which is very similar to the low density shelterwood. The lower mean germinant density for the seed tree method results from a combination of lower spring germinant density (SG) and the spring herbivory rate of 38 % (SH). As with the higher density shelterwood, the high variation in EG for the seed tree scenario is a legacy of the variation in the first season germinant population.

Discussion

Most forest regeneration modeling studies limit the scope of their investigation to single factors or a limited range of conditions related to influential factors. My model integrates multiple factors and allows us to further investigate interactions between various factors influential in recruitment, growth, and survival. This represents a more biologically cogent approach and provides a more thorough examination of the early recruitment process. For example, seed and safe site availability are often cited as

primary limiting factors to recruitment in forest ecosystems (Kellomäki *et al.* 1987, Eriksson & Ehrlén 1992, Peterson & Carson 1996, Cornett *et al.* 1998, LePage *et al.* 2000). While single factor analysis often supports these hypotheses and provides realistic model output, my modeling results suggest that combinations of factors working in concert represent the limitation to initial recruitment. For example, in examining the seed production levels and stand conditions, it appears that seed limitation is a barrier to recruitment only where seed tree densities are very low. Alternatively, at higher seed tree densities seed is limiting only in very poor or failed seed masting years (reference Tables 3.2 and 3.6). Seed limitations at the stand level result in part from the combined impacts that disturbance has on the health, distribution of seed trees, and the periodicity in seed production (Hubbell & Foster 1986, Schupp 1990, Greene and Johnson 1994). Disturbance, natural or managed, that result in residual seed trees with poor health or very low densities would combine with other factors such as safe site limitations and mortality to limit regeneration. The model and other field studies indicate that seed rain as a single factor is often poorly correlated with subsequent recruitment (Houle 1995). Thus a broader examination of combinations of factors provides a more complete explanation for initial recruitment outcomes. This illustrates the unique capacity of my model to expand the degree to which the regeneration process can be investigated for a single species, which previously was not available.

In general, the results from this study indicate that initial recruitment is strongly influenced by the interaction of three factors that broadly represent or influence seed availability within the recruitment sub-model (seed production, distance to plot, and stand structure represented by the two SD equations). My results are very similar to those reported by Schweiger & Sterba (1997) in their model for predicting Norway spruce regeneration as a function of seed tree density. Predictions for spruce regeneration were directly proportional to measures of seed availability. This outcome is not unique. Generally, in forest regeneration modeling propagule availability is cited as the driving force in predicting recruitment patterns in forests (Kellomäki *et al.* 1987, Peterson & Carson 1996, Greene & Johnson 2000). The trend in germinant recruitment rates follows a parabola whose slope is represented by the three factors contributing to seed availability (Figure 3.2a).

There are indications that seed limitations may occur as the seed tree density passes below the 9 m²/ha and become obvious at the 5 m²/ha. However, seed limitations predicted in these scenarios are not a sole function of seed tree density, but result from a combination of the decrease in seed production (i.e. decreasing WPBA), increases in distance from seed source, and variations in safe site availability. At very low seed tree densities, proximity to the seed source and availability of safe site and mortality may dominate. At higher levels of seed tree density the influential factors will shift, safe site availability may be limiting while proximity may be partially overcome by higher seed production rates. Indications are that although seed production is lower and distances from seed trees greater at the 5 m²/ha WPBA level, the general recruitment trends were very similar to the two shelterwood scenarios (Figure 3.5). This is likely related to the significant influence of mortality, differential safe site availability, and proximity to the seed source. In general, although variation levels for seed production appear large, there are few instances where seed limitations would represent a direct conflict to recruitment when stand structures are left largely intact. In this manner, the model supports the premise that shelterwood management is a viable regeneration technique (Hannah 1988). One inference derived from the model output is that when a majority of the forest canopy is removed, lower levels of seed production combine with variation in the distribution and availability of safe sites. This likely results in some degree of localized seed limitation and subsequently patchy regeneration. The interaction of the factors influential to seed availability may provide insight into observations for patchy recruitment patterns associated with isolated white pine stands in northern Minnesota. The model provides an opportunity to investigate recruitment patterns under varying conditions in a manner not previously available with other regeneration models. For example, the model provides an means by which specific site factors can be evaluated to determine the thresholds at which stand conditions may result in some degree of seed limitation. Patchy recruitment patterns are not unique to white pine communities but represent a well known and accepted limitation of the natural regeneration method (Greene & Johnson 2000, Greene 2000, Nyland 2002).

Recruitment patterns are strongly influenced by the impact disturbance patterns have on the residual structure and composition of the canopy (Greene et al. 1999). The

concurrent testing of the two seed dispersal equations provides information on the potential influence stand structure has on white pine recruitment patterns in combination with other influential factors (Table 3.3). Intact stands have a clear dampening effect on seed dispersal and recruitment in all but the immediate vicinity of the seed source (Geritz, de Jong & Klinkhammer 1984). Although not addressed in this study, the implication for recruitment in temperate forests is that species producing large quantities of light-weight wind dispersed seeds (i.e. *Betula* or *Populus* sp.) are less influenced by dampening effects of intact stands and could maintain a larger distribution pattern and compete for safe sites further from the seed source than white pine (Peterson & Carson 1996, Greene *et al.* 1999). In managed stands conflicts may arise between the efficacy of opening a stand to improve seed dissemination, establishment, and growth for a target species like white pine and the potentially aggressive response of competing vegetation to increases in the availability of light and other resources (Wagner 1994).

My model indicates that the importance of safe sites for the regeneration process varies with other factors, with outputs from the two tests indicating that recruitment increases correspond to increases in seed and safe site availability (Figure 3.2c, Table 3.6). Results from the seed tree scenario indicate that higher levels of safe site availability (mean = 60%) do not necessarily result in increased germinant recruitment. While the seed tree scenario has higher levels of safe site availability, the combined influence of lower seed availability, proximity, and factors such as mortality will limit recruitment. In this way, the model provides a unique way to examine a critical site factor such as safe site as it interacts with other key factors. As each species has unique requirements for germination and early establishment, availability of safe sites represents a significant sieve to the recruitment process (Schupp 1995, Greene 2000). In northern Minnesota safe site limitations likely result from a combination of historical changes in disturbance patterns, harvest methods, land use changes, and a shift in dominant cover types (Stine and Baughman 1992, Frelich & Reich 1995, Grigal & Bates 1997). For example, forest harvest practices that favor minimal disturbance to the forest floor and understory vegetation result in the creation of marginal levels of safe sites for white pine, subsequently established species will be favored regardless of seed availability (Lutz & Cline 1947, Wagner, Mohammed & Noland 1999). Conversely, an increase in the

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prevalence of green tree retention harvests may result in the creation of adequate safe site but insufficient seed availability for any one species.

One limitation of this model is the fact that it only permits investigation of conspecific seed sources and competition for safe sites, which represent ecologically unique circumstances. In mixed species stands, individual species represent a small proportion of the total seed source, and thus increasing diversity increases the complexity of regeneration dynamics. Theoretical and empirical reports indicate that when competition for safe sites is intense (i.e. high levels of species diversity), it will greatly influence recruitment rates for individual species (Geritz et al. 1984, Houle 1991, Eriksson & Ehrlén 1992, Greene et al. 1999). For example, following partial canopy harvest and site preparation treatments of a stand composed of 98 % white and red pine, white pine made up only 21% - 63% of the newly recruited seedlings and red pine was nearly absent altogether (Burgess & Wetzel 2000). It is therefore likely that my model overstates recruitment for white pine under all but the most favorable or unique combination of conditions. Expanding model construction to include multi-species influences represents a means to further investigate conflicts to species specific recruitment at the seed-germinant scale (Fowler 1988).

Once established, the combined influences of stand structure and composition begin to directly influence seedling growth patterns. The growth sub-model represents a unique tool to examine the height growth response as influenced by cover type and various combinations of competition (i.e. canopy closure, understory woody vegetation, and herbaceous). Mixed results are obtained from the model relative to the influence of herbaceous competition (i.e. ± coefficient values in Table 3.4). The mixed influence of herbaceous competition likely results from unique site factors and weeding techniques used in the case studies used to develop the equations (Appendix 2 and thesis Chapter 2). The practical impact of herbaceous competition is marginal and likely due to the muted growth response of these plants in shelterwood situations (reference Ch 2). Under more open conditions, the influence exerted by herbaceous competition would be greater (Wagner 1994). There is, however, a clear negative interaction between canopy closure, understory woody competition and height growth (Figure 3.3). Thus, the model predicts the largest growth rates when canopy closure is lowest combined with understory

conditions where woody vegetation is absent or controlled. In this manner, the model verifies observations from numerous shelterwood field trials which report the decline in growth rates as competition levels from overstory canopy closure and understory woody vegetation increase (Saunders & Puettmann 1999a, Puettmann & Saunders 2000, Wetzel & Burgess 2001). Thus, shelterwood operations that retain sufficient canopy closure to suppress understory vegetation in balance with the seedling requirements for light are preferred.

There is insufficient evidence from the model to determine if there are differential growth results specifically related to the influence of canopy composition as identified in other field studies (Counte 2000). Predictions for growth are very similar under the oak-maple and northern hardwoods cover types, but markedly lower under the conifer canopy. In general, the mesic hardwood sites support greater potential growth rates and thus potential levels of competition (Wendel *et al.* 1983, Stiell 1985, Wendel &Smith 1990). Specific differences in growth rates between the hardwood and conifer canopies likely result from the use of case studies conducted on different soils which posses unique combinations of resource availability, competitive influences, and site characteristics (Machado 1999, Counte 2000, Appendix 2). Thus species composition of the canopy may be less important than the overall productivity and competition levels on a given site. An inference drawn from the model and field studies indicate that reducing canopy closure levels provides an opportunity to promote growth under conifer canopies (Burgess & Wetzel 2000). Increasing canopy removal to promote seedling growth must be considered in light of the physiological needs of the seedlings and the potential increases in the density of understory vegetation, seedling mortality rates, and loss of vigor due to damage agents discussed in Chapter 2 of my thesis.

A significant limitation to the utilization of the growth sub-routine exists across each of the cover types tested. An analysis of model output reveals that predictions for height growth consistently exceed those reported for naturally regenerated germinants (Cornett 1996). This illustrates the operational limitation to using growth equations developed from studies of older, planted seedlings when white pine is known to have a slow growth rate during the first 3 to 5 years (Wendel & Smith 1990).

Poorly documented and understood mortality patterns in germinant communities are a significant source of variation in recruitment outcomes at various levels of scale (Smith 1940, Hocker 1961, Graber 1968, Cornett 1996, Cornett *et al.* 1998). Although mortality is only broadly characterized in this study, including some estimate for mortality provides a link and insight into an influential factor in short-term regeneration dynamics (Hocker 1961, Graber 1968). Clearly, the statistical significance of initial mortality in this study is tied to the wide range of mortality values tested (40 – 90% in the sensitivity test). Reducing the range (distribution) for initial mortality levels would reduce the overall impact this factor exerts on subsequent germinant density and thus its significance to the model.

The interaction of site-specific characteristics and stochastic processes account for the majority of variation related to specific mortality agents (Smith 1940). Principle agents for 1st and 2nd year seedling mortality are: incomplete emergence, drought, heat injury, damping off, insect and mammal herbivory (Smith 1940, Graber 1968). Distance dependent mortality is not associated with germinant communities (Houle 1995). Disturbance to the canopy and forest floor have a significant influence on germinant mortality patterns (Wagner 1994). Under open canopy conditions the forest floor remains drier and greater fluctuations in temperature and moisture conditions occur. In open conditions drought and heat related injuries would be expected to increase and mortality due to damping off would decrease. In closed canopies, understory environmental conditions may remain relatively unchanged and mortality due to moisture stress would decrease and disease elements would increase (Smith 1940). For example, reports of mortality rates for planted seedlings consistently declined following partial removal of the canopy and after site preparation or vegetation management, i.e. weeding treatments (Saunders & Puettmann 1999a, Man & Lieffers 1999, Wetzel & Burgess 2001). It is important to note that beyond the first two or three years, mortality patterns (i.e. causative agents) in seedling-sapling populations shift to density dependent influences such as competition (Smith 1940, Houle 1995).

The sub-models independently, or in combination, represent a powerful tool to examine regeneration processes. In this study, two specific versions of the model were tested and evaluated (deterministic and stochastic). Each version appears to provide a

reasonable means to investigate relationships between factors and output related to the short term establishment of germinants. However, there are important limitations related to predictions for height growth and the capacity to model multiple species competition for safe sites. An asset associated with using this modeling technique is that it incorporates generic regeneration factors common to temperate species, which are adaptable to a range of potential stand conditions. The sub-models can be modified to predict regeneration patterns for other species by altering the variable selection, parameterization, and stand conditions unique to a regeneration scenario. For example, where specific information is available on the incidence of a specific mortality agent like damping off, the mortality variable can be modified with the applicable empirical function. The frame based modeling approach used in this study is inherently flexible and each sub-model has the capacity to operate independently.

In terms of application, there may be an opportunity to expand the use of this model to conduct retrospective analyses of regeneration outcomes by operating the model through reverse time steps. A retrospective analysis may provide an opportunity to refine the parameterization process for individual factors under specific stand conditions and examine the interaction of sets of variables. This may be one means by which limitations or knowledge gaps related to specific factors may be overcome. To expand the utility of the model, the framework can be expanded to a multi-species regeneration model that incorporates density dependent competition and mortality functions in more than just the initial two years.

Conclusion

As a tool to examine regeneration dynamics, the model appears to function logically and yield results that conform to the silvicultural understanding for white pine. Although a full verification process is beyond the scope of this study, the model seems to represent a viable tool to examine and integrate information on short term recruitment patterns, height growth, and mortality. The technique of combining disparate information into a single study to parameterize a model appears merited when specific controls on bounding factors are implemented. The application of this technique as an analysis tool for the integrated analysis of forest regeneration processes will be aided as additional species specific regeneration studies are conducted and reported. A limitation identified

in the conduct of this study, and observed in other recruitment modeling studies, is that there continues to be a lack of detailed, critical information necessary to parameterize a model that employs this level of detail (Robinson 1998, Greene *et al.* 1999). Additional research efforts will be required to overcome this limitation.

The broad variation in recruitment and early growth outcomes identified in temperate forests and modeled in this study are the result of the combined interaction of many factors such as stand composition, seed production, safe site availability, mortality patterns, and competition levels (Logan 1959, Lancaster & Leak 1978, Houle 1991, Cornett 1996). Although seed and safe site availability have a significant impact on recruitment, it is the combined influence of multiple factors that determine regeneration outcomes for a given site. Predictions for germinant densities in the first two years illustrate the high level of variation inherent in germinant communities that result from numerous stochastic interactions and micro-site conditions (Greene *et al.* 1999). I recommend expanded hypothesis testing under a range of stated site conditions to provide additional information on potential seed-safe site conflicts that occur in northern Minnesota.

Using the model to evaluate management alternatives may prove a useful tool to natural resource managers. The model provides a means to evaluate combinations of factors that act as ecological filters or promote critical phases of the regeneration process: seed survival, germination, and early survival and growth (*sensu* Schupp 1995). For example, management actions that rely on higher residual seed tree density levels to increase germinant density is likely inadequate and ignores other significant factors influenced by this activity (Kershaw 1993). The influence of stand structure on plant vigor, seed production, distribution, and post-harvest site conditions that include species mix, are significant and will combine to influence recruitment outcomes (Schupp 1995). Model output from this study indicates that even when low levels of seed tree density remain following a disturbance, seed availability may prove sufficient to maintain a semblance of short-term conifer presence at the germinant stage when mortality levels are not high and some quantity of safe site is available. Long term stochastic and density dependent factors will eventually determine the maintenance of conifer cover at a given site. When germinant populations in the first or second year are very low (e.g., < 50/ha)

mortality functions in succeeding years may exert sufficient influence to result in regeneration outcomes where white pine is absent from the understory (Smith 1940). In some cases, however, low initial recruitment levels can support an ongoing presence as a result of facultative gap capture processes (Abrams 2001).

In the process of constructing and parameterizing the model, a number of gaps in the regional knowledge base have been identified. For example, growth equations developed from experiments with planted stock do not adequately reflect early growth patterns in naturally regenerated seedlings. Investigating growth patterns in naturally regenerating germinants may provide insight into the role stand conditions play at such a young age. Further testing will determine whether this series of equations may be used to model height growth in white pine plantation forests. Research efforts that investigate the stochastic processes in germinant communities will add to our understanding of the regeneration process and the reliability and accuracy of this and other process models.

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Table 3.1 Notation used for factors in the model.

Sub-model and Variables	Notation
Recruitment	
white pine BA	WPBA
seed year generator	SYG
masting cycle	MC
seed production	SP
seed viability	SV
seed distribution	SD
distance to plot	DP
seedfall	SF
seed predation	PD
safe site	SS
initial germinants/plot	IG
mortality	IM
germinants	GT
Height Growth	
initial height	IH
overstory canopy closure	OCC
understory competition	UC
% herbaceous cover	HB
end of season height	ESH
Mortality	
second year germinants	SG
winter mortality	WM
spring herbivory	SH
summer mortality	SM
ending germinants	EG

Table 3.2 Values used to parameterize the recruitment sub-model in the sensitivity test.

seed tree m²/ha	seed production/ha low/high	seed viability	seed distribution equation	distance to plot	seed predation	safe site	initial mortality rate
10	750,000	.60	inside stand	5 or 60 m 25 or 200	.25	.20	.40
	1,400,000	.95	outside stand	m	.75	.80	.90
28	2,000,000	.60	inside stand	5 or 60 m 25 or 200	.25	.20	.40
	3,400,000	.95	outside stand	m	.75	.80	.90
43	1,300,000	.60	inside stand	5 or 60 m 25 or 200	.25	.20	.40
	2,000,000	.95	outside stand	m	.75	.80	.90

Note: for the purposes of this test the masting cycle variable was not used.

Table 3.3 Results from the recruitment sub-model sensitivity test. Germinant densities (per hectare) are reported as a function of seed tree density and the seed distribution equation.

seed tree density (m^2/ha)	10		28		43	
seed distribution equation	IS	OS	IS	OS	IS	OS
germinants/ha						
mean	16.600	22.000	42.100	55.100	26.100	33.500
sd	33.300	46.100	84.200	114.100	52.000	68.800
high value	137.200	337.300	333.100	819.300	481.900	481.900
low value	100	100	300	300	200	200

IS = inside stand distribution equation [2], (SD)

OS = outside stand distribution equation [3], (SD)

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Table 3.4 Parameter settings and equation coefficient values used in the sensitivity test of the growth sub-model. The df represents the degrees of freedom associated with the development of the growth equation by cover type.

cover type	intercept	initial height (cm)	height coefficient	OCC	OCC coefficient	UC	UC coefficient	HB %cover	HB coefficient	OCCXUC interaction
conifer	20.21	10	1.2	0.3	-17.97	0	-2.76	0	0.04	3.46
df= 417		40		0.9		1		75		
n. hardwood	23.46	10	1.24	0.3	-16.39	0	-4.45	0	-0.02	5.57
df= 804		40		0.9		1		75		
oak-maple	19.09	10	1.11	0.3	-11.77	0	-2.46	0	-0.04	2.48
df= 812		40		0.9		1		75		

Table 3.5a Analysis of variance sensitivity test results for the recruitment sub-model. Dependent variable is initial year germinants (GT).

Parameter	df	Type III SS	Variation Explained (%)	F-Value
SP	1	19400872	10	29
SV	1	4674510	2	7
SD	1	11499897	6	17
DP	1	50047922	27	74
SS	1	33003949	18	49
PD	1	22919409	12	34
IM	1	46774304	25	70

Table 3.5b Analysis of variance sensitivity test results for the height growth sub-model. Dependent variable is the end of season height (ESH).

Parameter	df	Type III SS	Variation Explained (%)	F-Value
cover type	2	245	2	37
IH	1	15123	95	4461
OCC	1	511	3	151
UC	1	25	<1	7
HB	1	3	<1	0.88
OCC*UC	1	16	<1	5

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Table 3.6 Variable settings used in the model application test and output indicating predicted germinant density and height. Output variables are indicated in bold and result from differences in the values tested among the three silvicultural scenarios.

sub-model and variable	shelterwood 9 mean	shelterwood 9 variation	shelterwood 19 mean	shelterwood 19 variation	seed tree 5 mean	seed tree 5 variation
Recruitment sub-routine						
white pine basal area	9		19		5	
seed viability (constant) ♦	0.8		0.8		0.8	
distance to plot (m) ♦	11	6.12	11	6.12	22.5	11.9
seed predation ♦	0.375	0.085	0.375	0.085	0.375	0.085
safe site ♦	0.5	0.102	0.375	0.085	0.6	0.136
initial mortality ♦	0.5	0.102	0.5	0.102	0.5	0.102
Output						
predicted germinant/ha (GT) #	**29,800**	**7,900**	**42,600**	**48,100**	**21,200**	**24,800**
Growth sub-routine						
intercept *	20.23	2.8	20.23	2.8	20.23	2.8
initial height (cm) # ♦	4.9	0.1	4.7	0.1	5	0.1
IH coefficient *	1.2	0.04	1.2		1.2	0.04
overstory canopy closure ♦	0.40	0.136	0.55	0.1	0.10	0.06
OCC coefficient *	-17.97	2.88	-17.97	2.88	-17.97	2.88
understory competition ♦	0		1		0	
UC coefficient *	-2.76	2.77	-2.76	2.77	-2.76	2.77
% herbaceous cover (constant) ♦	10		70		70	
herb coefficient *	0.04	0.013	0.04	0.013	0.04	0.013
interaction coefficient (OCC X UC) *	3.46	3.27	3.46	3.27	3.46	3.27
Output						
end of season height (ESH) (cm) #	**19.6**	**3.7**	**18.1**	**5.0**	**27.2**	**3.1**
Mortality sub-routine						
initial germinants/plot #	298	79	426	481	212	248
winter mortality ♦	0.25	0.034	0.25	0.034	0.25	0.034
spring herbivory (constant) ♦	0.5		0.25		0.38	
summer mortality ♦	0.35	0.102	0.35	0.102	0.35	0.102
Output						
end yr 2 germinants/ha (EG) #	**10,800**	**1,400**	**17,800**	**15,100**	**8,600**	**10,100**

* coefficient estimate +/- se
\# mean +/- sd
constants were tested at the value indicated
♦ hypothesized value and distribution
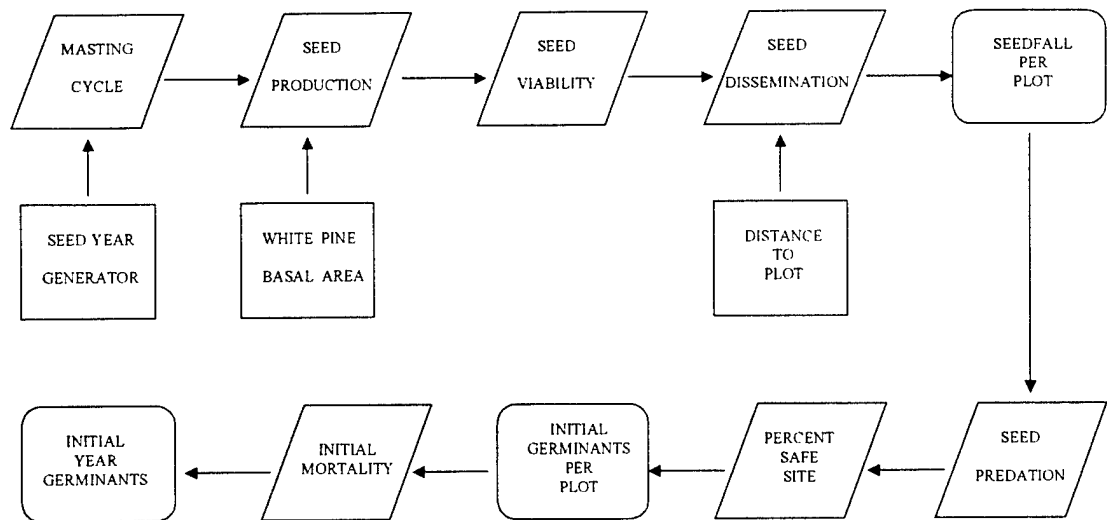per/plot X 100 = per/ha

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Figure 3.1a Diagram of the recruitment sub-model as utilized in the model application test. The seed year generator and the masting cycle are omitted in the sensitivity test. **Legend:** Arrows with solid lines indicate the sequential flow of the model. Squares represent stand conditions input by the user or generated by the program, parallelograms represent processes or functions, and rounded rectangles represent interim results and output variables.
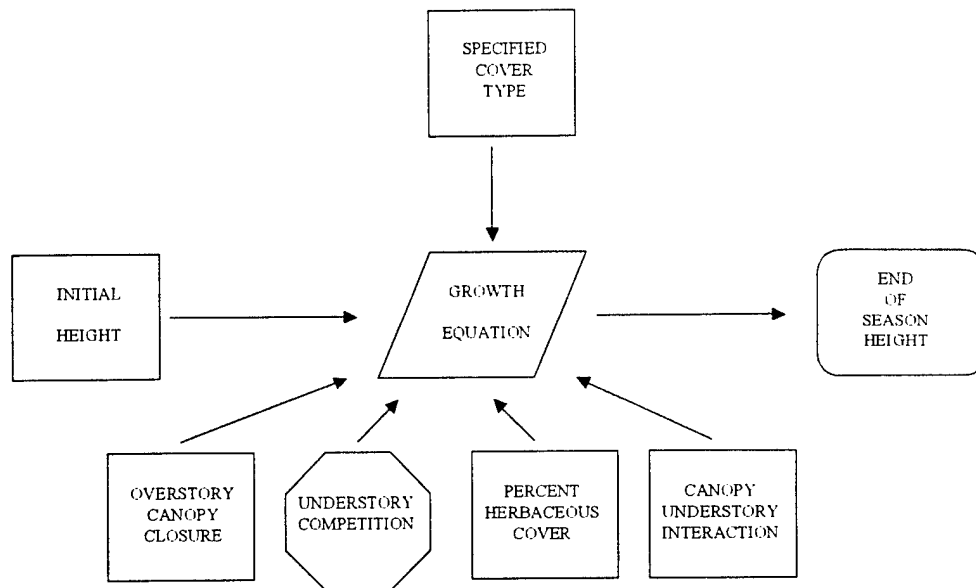
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Figure 3.1b Diagram of the growth sub-model. The specification of cover type determines the values for equation coefficients. **Legend:** Arrows with solid lines indicate the sequential flow of the model. Squares represent stand conditions input by the user, parallelograms represent processes or functions, octagons represent categorical variables, and rounded rectangles represent interim results and output variables.
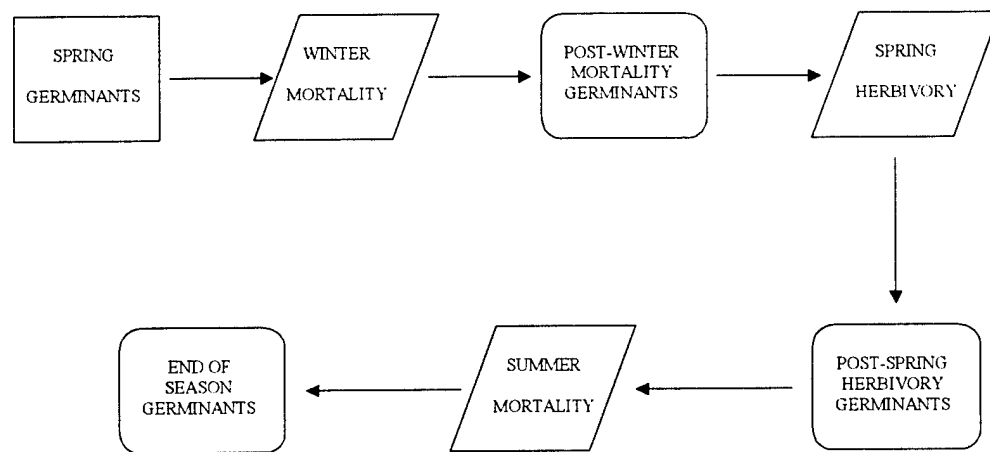
Figure 3.1c Diagram of the mortality sub-model. **Legend:** Arrows with solid lines indicate the sequential flow of the model. Squares represent stand conditions input by the user, parallelograms represent processes or functions, and rounded rectangles represent interim results and output variables.
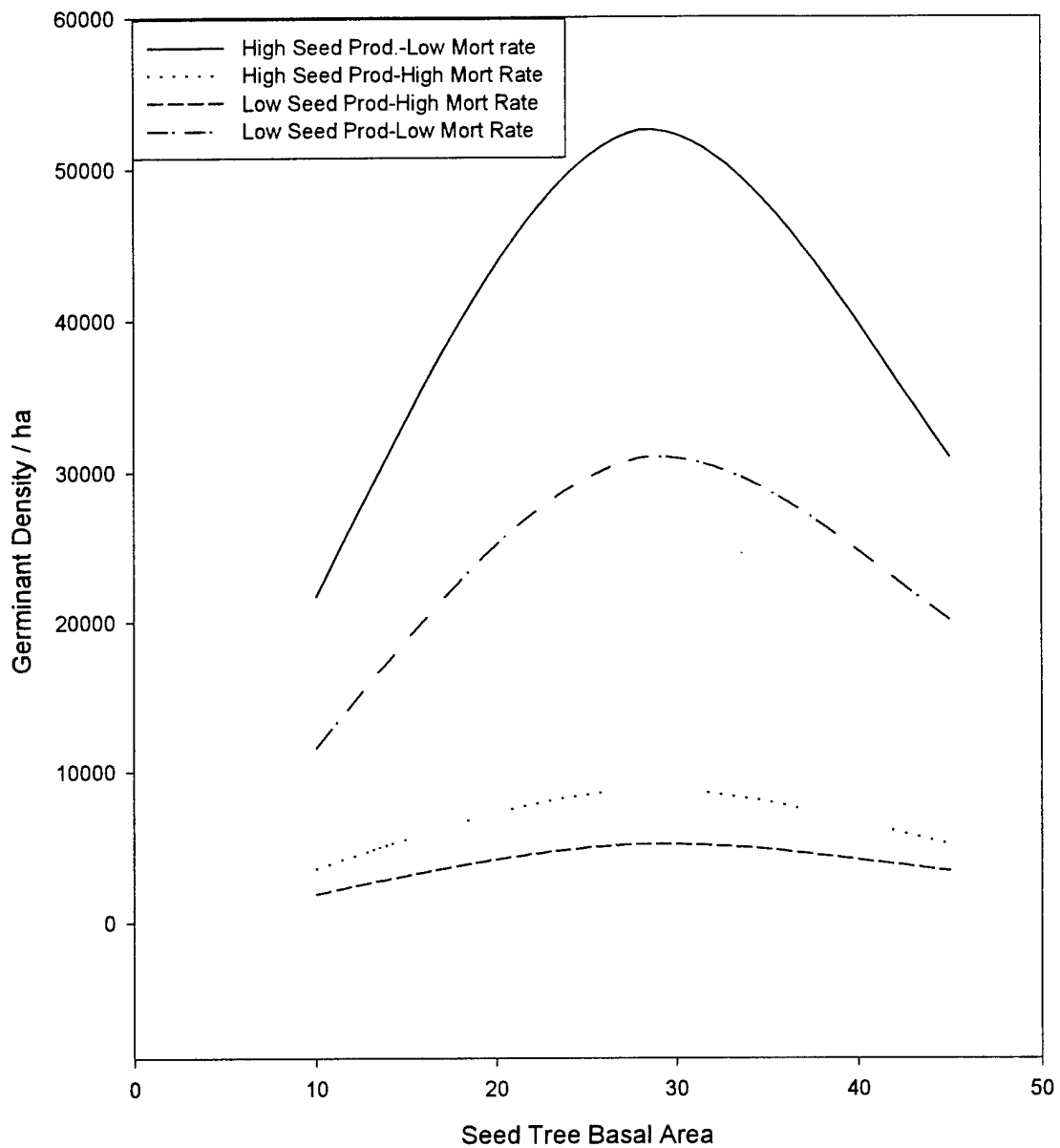
Figure 3.2a Plot of germinant density as a function of seed tree basal area, within-stand seed dispersal, seed production rate and mortality. Values held constant: distance = 25 m, safe site = 20 %, viability = 0.6, seed predation = 25%.
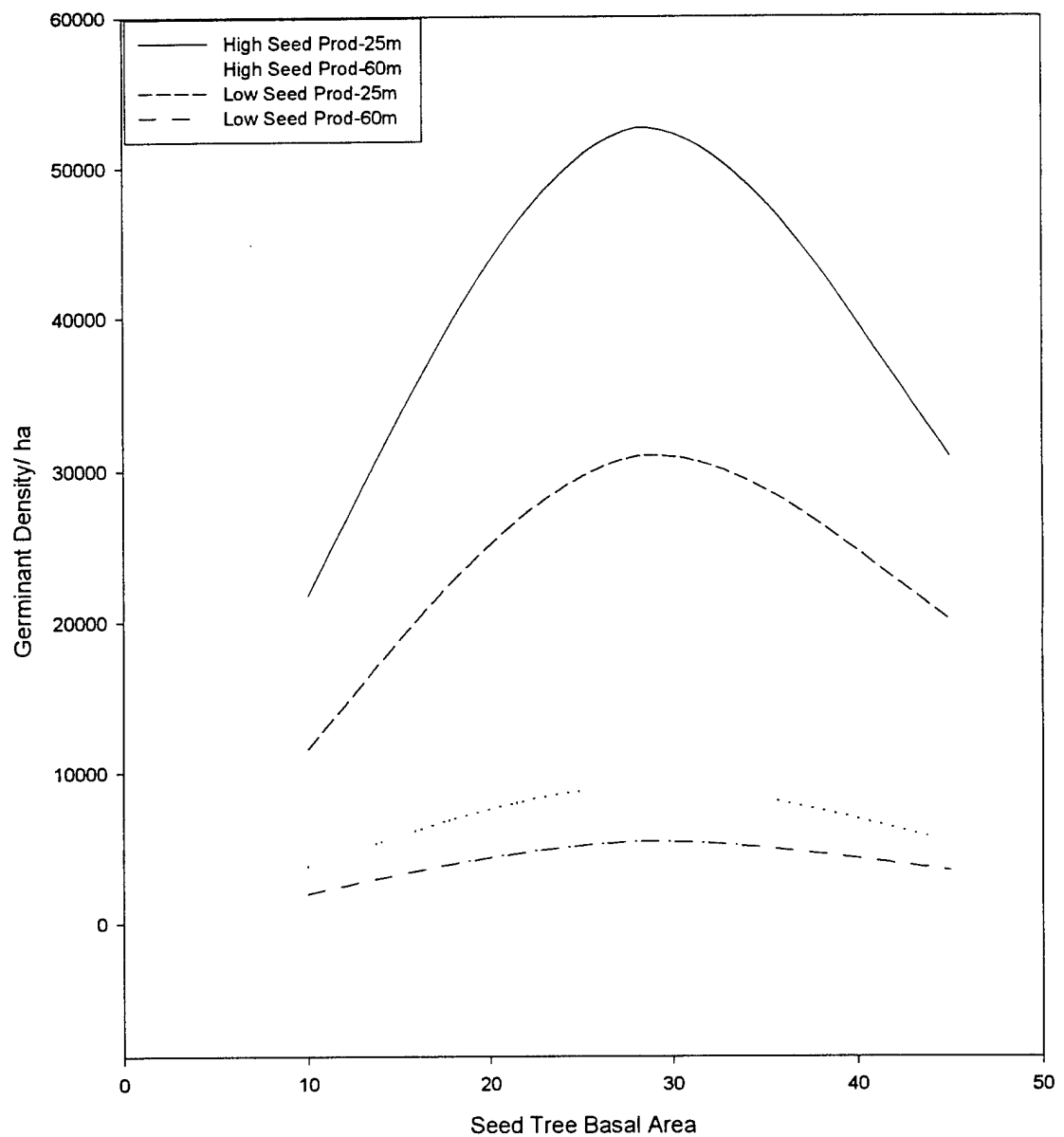
Figure 3.2b Plot of germinant density as a function of seed tree basal area, within-stand seed dispersal, seed production rate and distance to plot. Values held constant: mortality = 40 %, safe site = 20 %, viability = 0.6, seed predation = 25%.
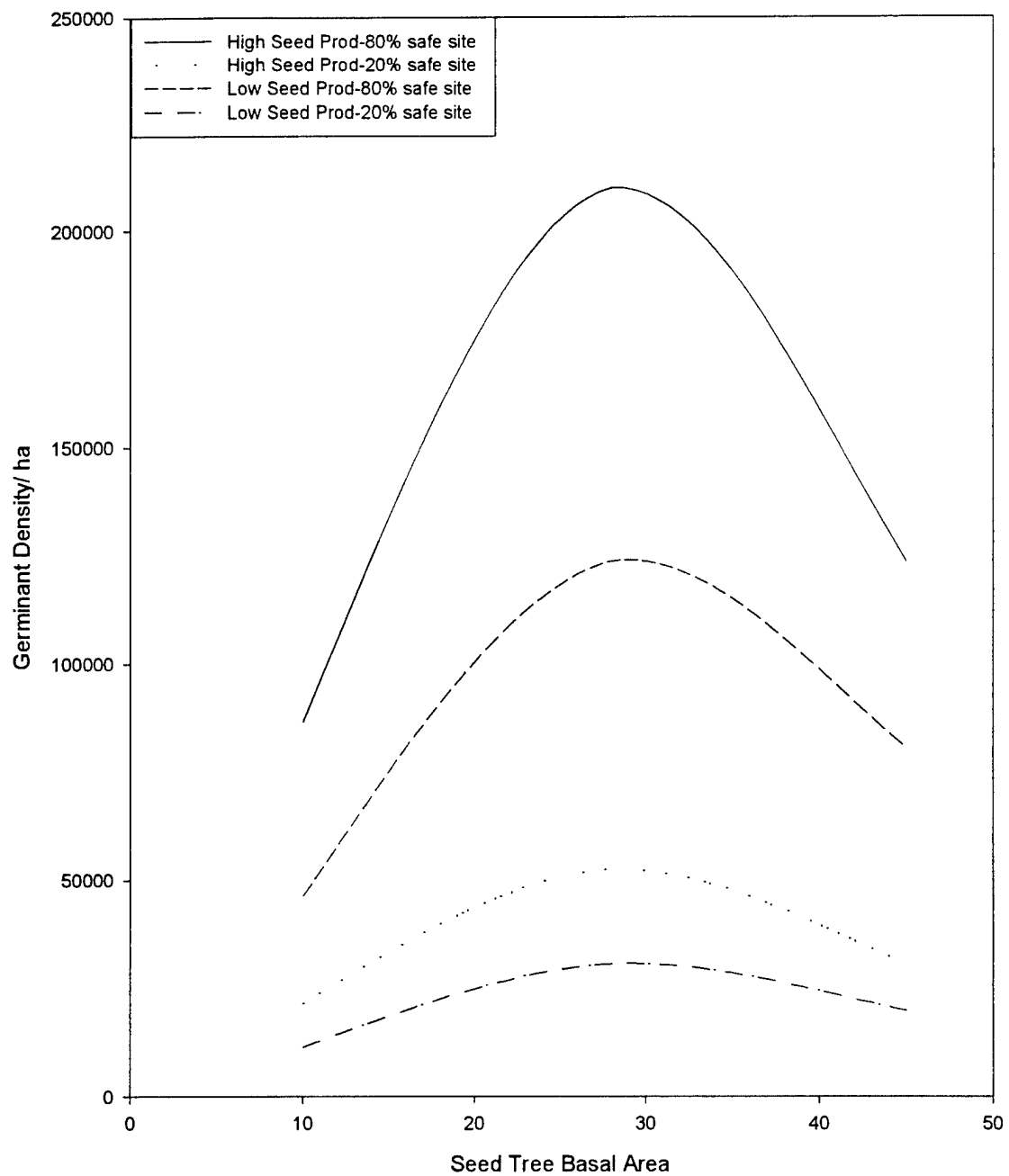
Figure 3.2c Plot of germinant density as a function of seed tree basal area (m²/ha), within-stand seed dispersal, seed production rate, and safe site. Values held constant: mortality = 40 %, distance = 25 m, seed predation = 25 %, viability = 0.6.
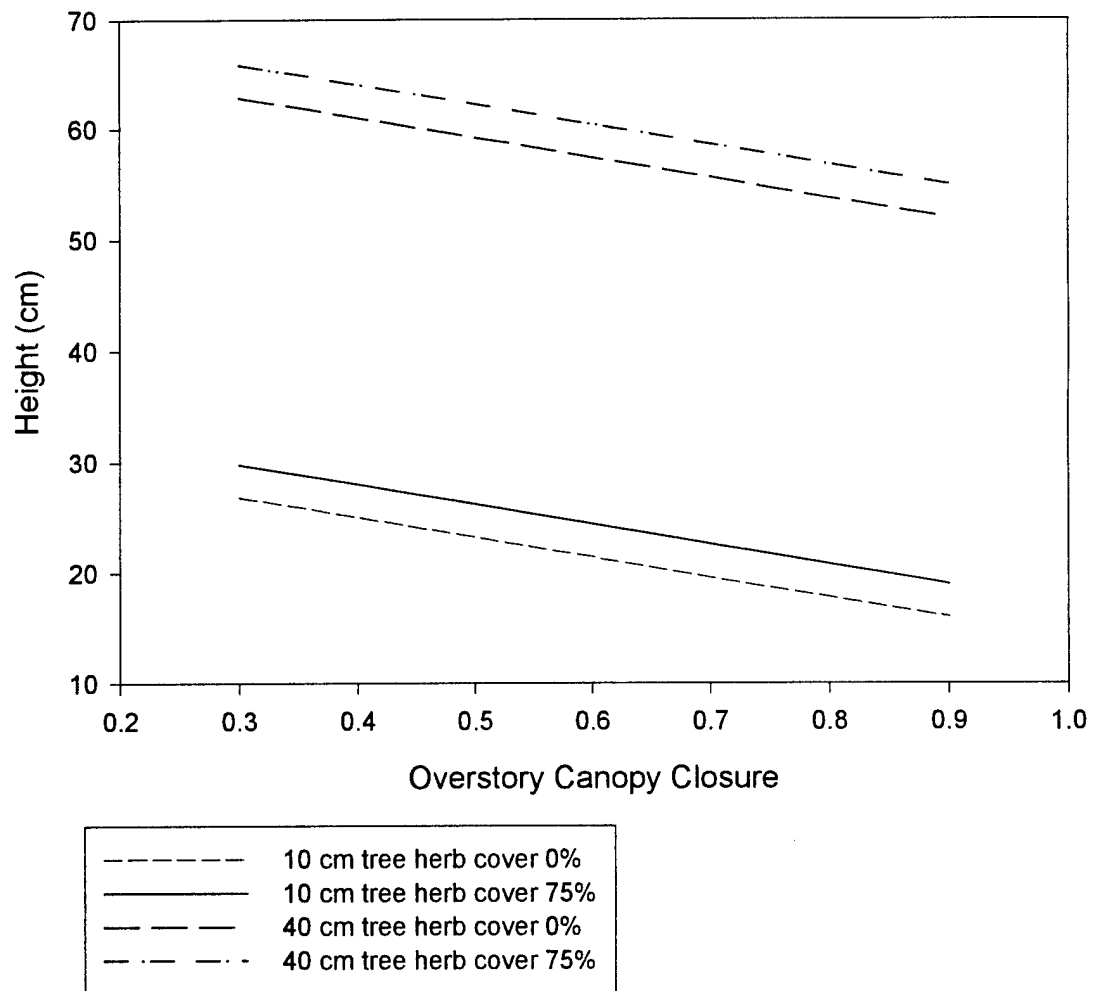
Figure 3.3 Plot of the height growth sensitivity test results for the conifer cover type. The plot illustrates the relationship between end of season germinant height (ESH) as a function of initial height (IH = 10 cm or 40 cm), overstory canopy closure (OCC), and percent herbaceous cover (HB). The understory competition (UC) is set to 1 to include the influence of understory woody competition. Note: for the conifer cover type herbaceous cover has a slight positive impact on growth.
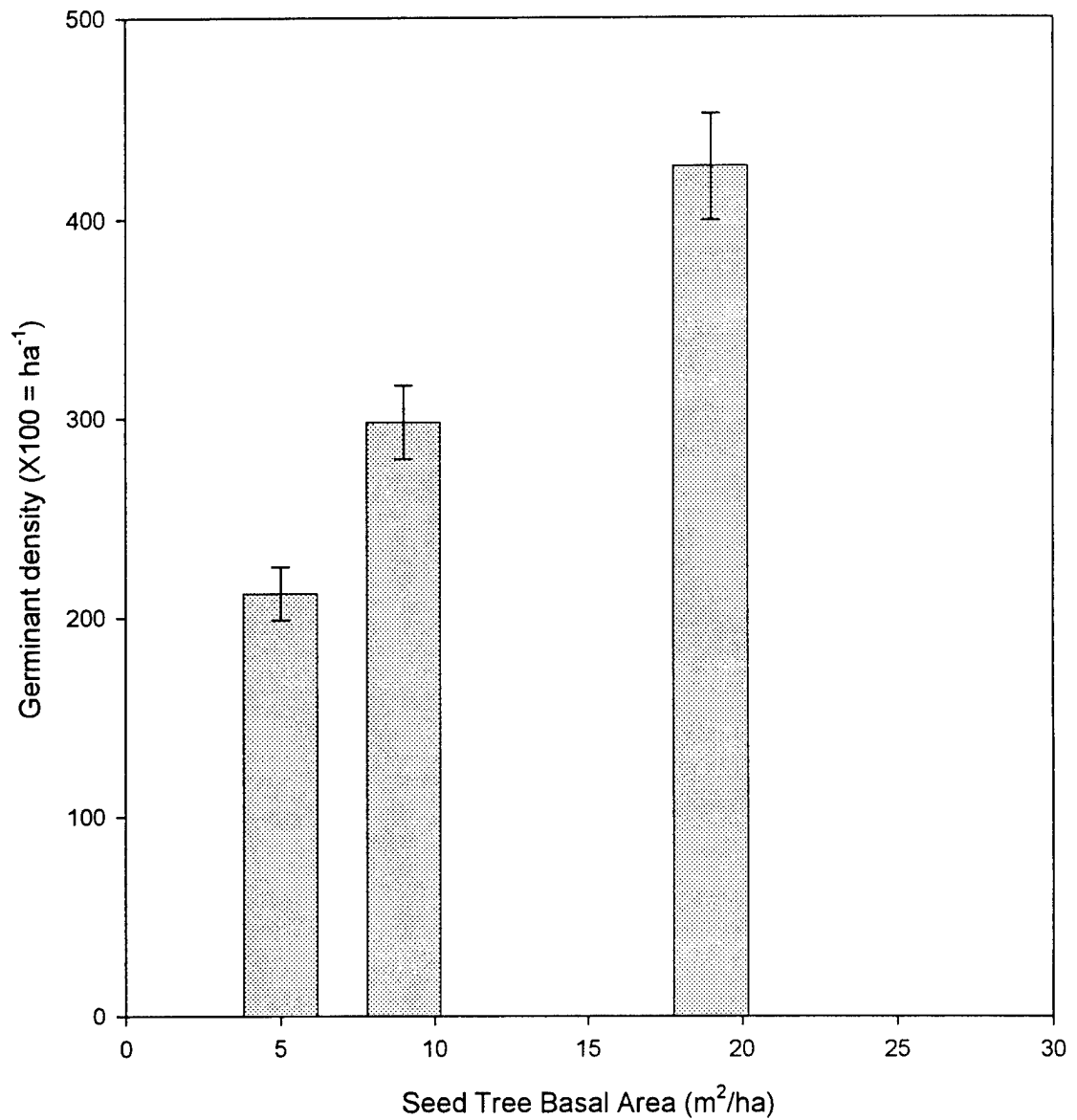
Figure 3.4a Plot of the 95% confidence interval for the results from the model application test for germinant density (GT) as a function of differential seed tree density (WPBA), safe site (SS), distance to plot (DP) and seed dissemination equation (SD). Germinant densities increase relative to seed availability as a function of seed tree density. Reference table 3.6 for specific values tested.
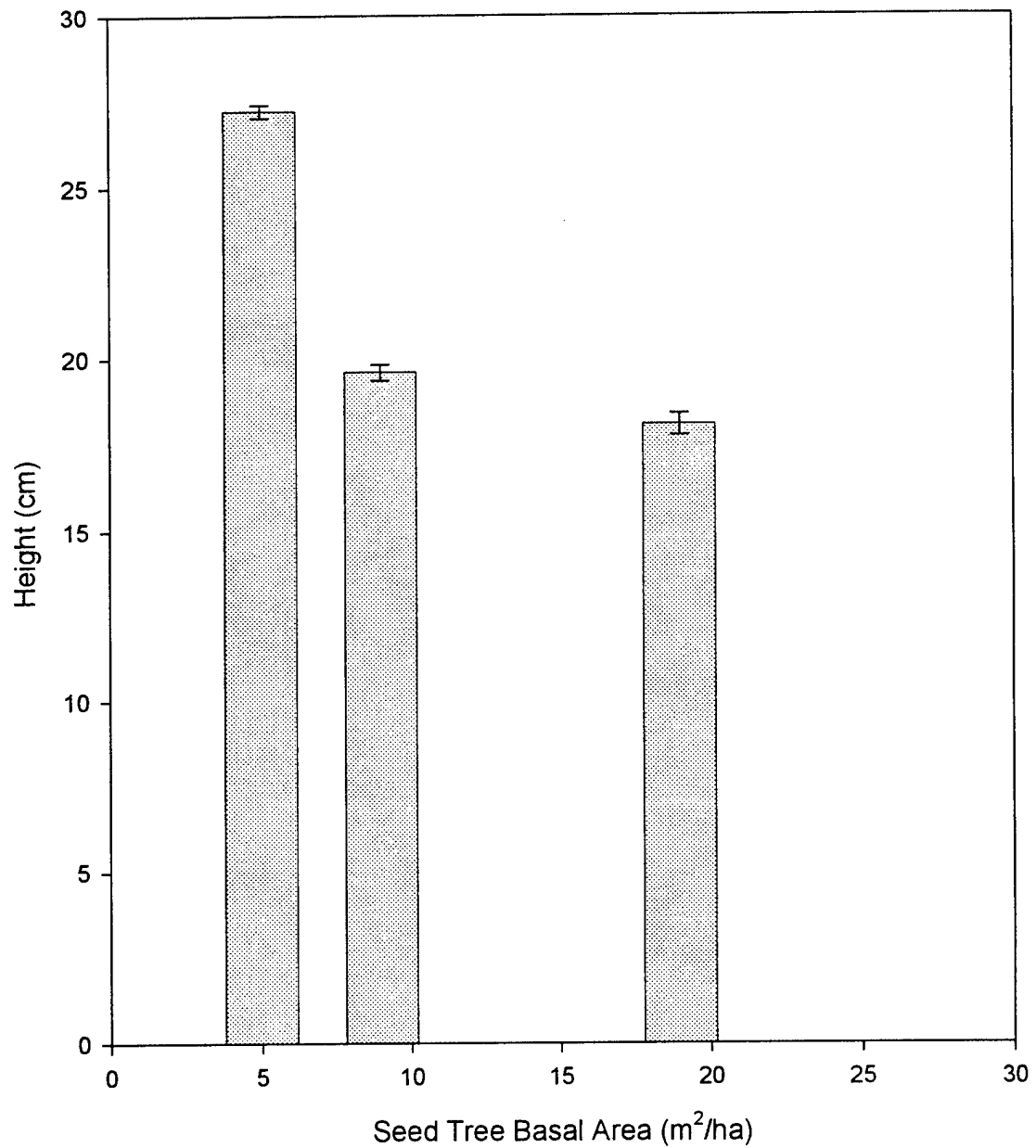
Figure 3.4b Plot of the 95% confidence interval for the results from the model application test for end of season height (ESH) as a function of competitive influences. There is a clear difference in the mean height in the 5 m^2/ha scenario, however it is not possible to determine a true difference exists between the 9 m^2/ha and the 19 m^2/ha scenarios.
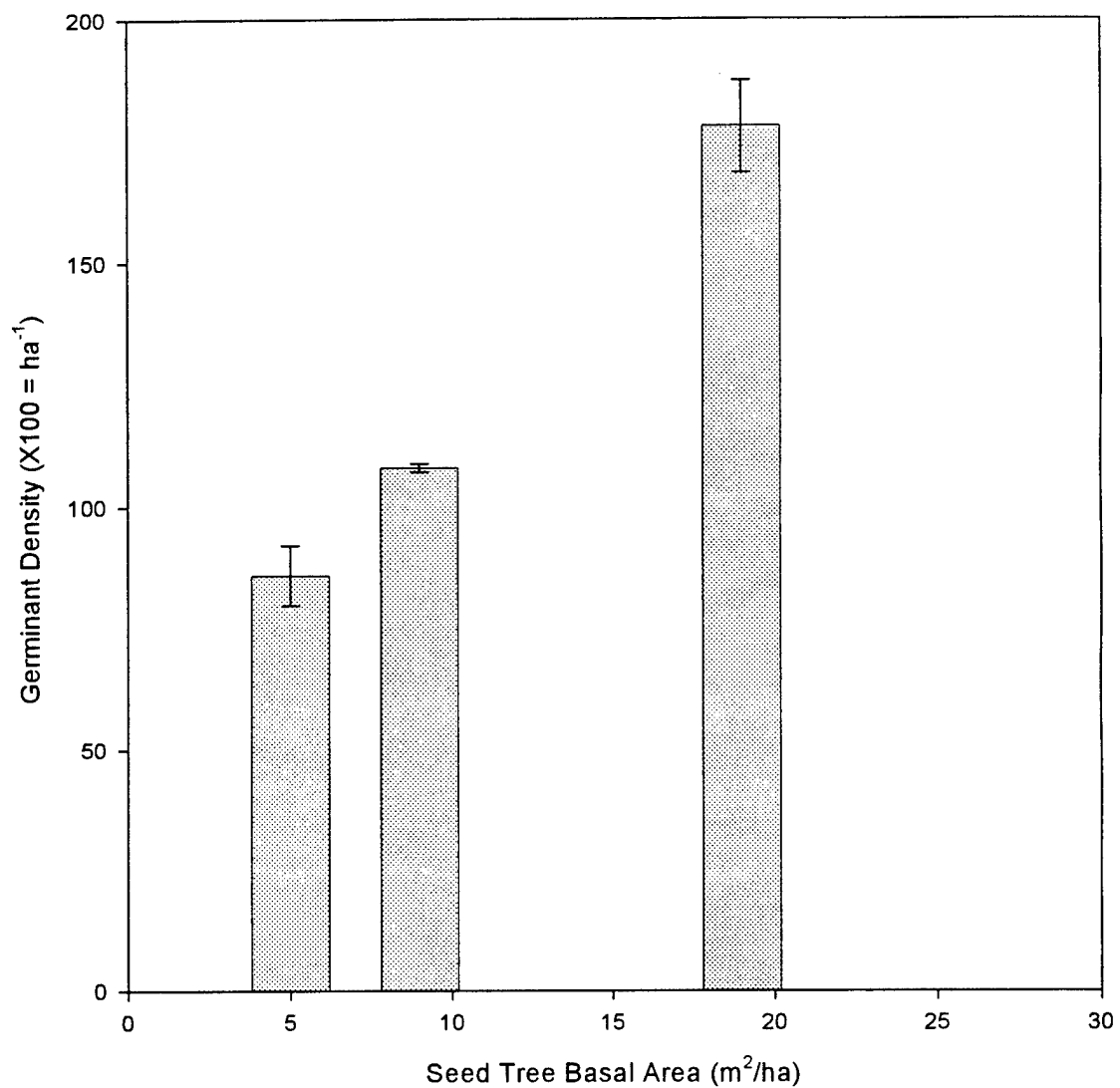
Figure 3.4c Plot of the 95% confidence interval for the results from the model application test for mean germinant survival in the second season (EG) as a function of differential mortality from spring herbivory (SH). The trend towards congruency in germinant densities between the 5 m²/ha and the 9 m²/ha scenarios has developed as a result of herbivory. Reference table 3.6 for specific values tested.
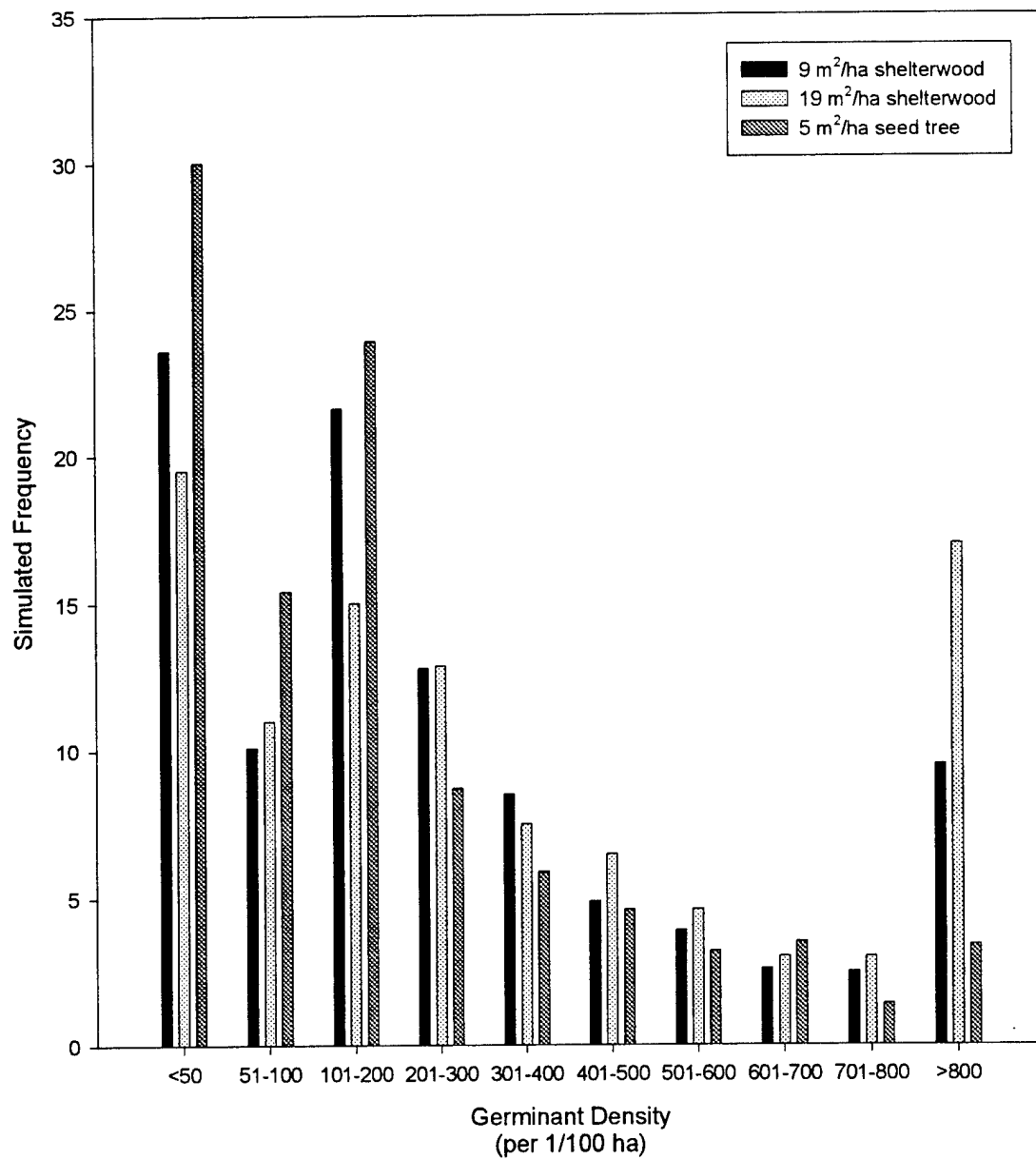
Figure 3.5 Simulated frequency of occurrence of first year germinants (GT) by germinant density category as a function of seed tree density (WPBA), seed distribution (SD), and safe site (SS). Based on 1000 iterations of the recruitment sub-model. Reference table 3.6 for specific values tested.

Appendix 1

Descriptions of variables, parameterization, sources and assumptions

This appendix presents information related to model construction. Variables are defined and relationships identified. Information on sources used to parameterize variables and test the model are supplied and assumptions are provided. Bounding functions for each variable as used in the model application test describe an upper and lower limit that were developed using the entire range of data sources available as recommended by Dolph & Dixon (1993). An assumption of the model is that no extreme climatic or disturbance events occur.

Recruitment model (Figure 3.1a)

White Pine Basal Area (WPBA): A value input by the model user to represent overstory white pine density in m^2/ha. Basal area is defined as the sum of the cross sectional area of all stems measured 1.37 m above ground averaged on a per area basis (Helms 1998). The value for WPBA represents a measure of overstory density that influences seed production and distribution. Specifically, WPBA is used to define a range of seed production as described in the seed production variable (SP). The model assumes that the value for WPBA represents healthy, vigorous, seed producing white pine canopy trees evenly distributed across the site.

Seed Year Generator (SYG): This variable is an evenly distributed random number generator bounded by 1 and 100 whose value determines the masting cycle category. The association between SYG and MC is as follows: SYG 1-20 = failure, 21-29 = bumper, 30-50 = good, and 51-100 = moderate.

Masting Cycle (MC): This variable represents the influence of seed masting cycles on seed production (SP). Four masting cycle categories are used: bumper, good, moderate, and failure. The specific category for masting cycle is determined by the random number generated in the seed year generator. The long-term frequency of occurrence for each

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MC category is: failure 20%, moderate 50%, good 22%, and bumper 8%. Each MC category represents a normally distributed random variable that corresponds to a range of seed produced (SP) as a proportion of the maximum potential seed production per unit of seed tree density (Appendix 1). The range of seed production by MC category is: failure 0.1 % (low) to 3 % (high) of maximum, moderate 4 % (low) to 25 % (high) of maximum, good 26 % (low) to 74 % (high) of maximum, and bumper 75 % (low) to 100 % (high) of maximum.

Masting cycles for white pine are reported in Graber (1970) Lancaster & Leak (1978), Stiell (1978), Godman & Mattson (1985), Krugman & Jenkinson (1989), Wendel & Smith (1990), and Young & Young (1992). Additional information on the quality of 42 seed years for white pine was supplied by the Canadian Forest Service (unpublished data, Petewawa Research Forest). This variable is used in the model application test only.

White Pine Seed Production (SP): This value is calculated directly or interpolated from Graber (1970) and unpublished data from the Canadian Forest Service (S. D'eon and W. Parker pers. communication). Using the WPBA a range of the number of seed produced per hectare is calculated. The two specific methods to calculate SP are described in the sensitivity and model application test.

Seed Viability (SV): Seed viability refers to the germanitive capacity of seed. Specifically it represents the physiological capacity of the seed to germinate and produce a functioning cotyledon. Seed viability in white pine varies by seed release date, seed mass, masting cycles, and seed tree vigor. For the purpose of this study, seed viability represents the mean seed viability rate for that year's seed crop. Sources used to determine typical white pine seed viability include Graber (1970), Stiell (1978), Krugman & Jenkinson (1989), and the Canadian Forest Service (unpublished data).

Seed distribution equation (SD): Seed distribution is an equation that represents the influence of the residual stand structure on the dissemination of seed. Seeds disseminated within a stand are not spread as far as those spread outside a stand. Two distribution

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equations were developed from a simple negative decay curve to represent within-stand [2] and outside-stand seed distribution [3]. Symmetrical seed distribution is assumed with no physical barriers to seed dispersal and no differentiation for distribution by cover type. The distance value (DP) used in the equation is described below. The seed distribution equation is based on recommendations for wind dispersal of winged seeds by Okubo & Levin (1989), Rudis, Ek & Balsiger (1978), and Wendel and Smith (1990).

Distance to plot (DP): A range (or single distance) input by the user to represent the normal range of distances (m) from the seed source to the point where seeds land. This variable is a function of the stand density and site conditions. Incorporating this variable allows a limited investigation of elements related to spatial variation when multiple iterations for various distances are run and results combined.

Seedfall (SF): This variable represents the quantity of viable seed that lands in the plot. The model assumes symmetrical seedfall.

Seed predation (PD): Seed predation is expressed as a proportion of viable seed produced (SP*SV) that is consumed or removed by predators. Seed predation is a highly variable and often localized process. It is, in part, a function of stand conditions and population dynamics of a range of small mammals and bird species. Insect predation on cones is not modeled. Information used in this model to predict seed predation rates comes from Abbot (1961), Hocker (1961), Graber (1969), Abbot (1970), Heckman, Pecore & Sloan (1986), Vander Wall (1992), Cornett *et al.* (1998), Duchesne *et al.* 2000, and unpublished data from the Canadian Forest Service (S. D'eon and B. Parker pers. communication).

Safe site (SS): Safe site is a variable that represents the proportion of total plot area (100 m^2) that will support germination and early establishment (1st two years). The overall concept of safe site is defined by Green (1983), Geritz *et al.* (1984), and Fowler (1988). In essence, it describes the relative receptiveness of the site where seeds are deposited in terms of suitability for successful seed germination and early survival (*sensu* Schupp

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1995). A favorable safe site enhances germination and early survival and growth. Safe site, as used in this study, does not preclude mortality as a function of seed or seedling predation, herbivory, or other biotic/abiotic factors that occur in the first two years.

Initial Germinants (IG): Germinants resulting from viable seeds deposited on a safe site not removed by predation. It is assumed that viable white pine seeds, not subject to predation, deposited on safe sites will germinate.

Mortality (IM): A variable that represents the proportion of the total population of initial germinants (IG) that die in the first season following germination. Modeling mortality as a proportion of the population is recommended by Lee (1971) and Hann (1980). IM collectively summarizes the proportion of the germinant population removed by a wide range of sources such as: climatic factors, desiccation, drought, heat injury, insect and small mammal predation, herbivory, disease, and mechanical damage. Each mortality factor is a function of large and small-scale climate patterns, stand history, disturbance patterns, structure, and local population dynamics.

Sources used to establish the bounding properties for germinant mortality include reports by Smith (1940), Hocker (1961), Graber (1968), Cornett (1996), Cornett et al. (1998), Saunders (1998), unpublished data from our Silviculture Lab (i.e. Two Harbors database from Chapter 2), and unpublished data from the Canadian Forest Service in Ontario (S. D'eon and B. Parker unpublished data). Based on broad generalizations for specific mortality agents of germinants described in the literature, I do not attempt to specify causation for mortality. Mortality associated with diseases such as white pine blister rust (Cronartium ribicola) are not utilized. Blister rust, although a significant element in mortality of white pine stands, is not reported in germinants.

Germinants (GT): The density of germinants at the end of the year of establishment.

Growth sub-model (Figure 3.1b)

Initial Height (IH): Initial height is set by the user and represents the height (cm) distribution of the germinant population produced by the recruitment sub-model at the end of the first growing season (GT). Height values used in this study were obtained from unpublished data supplied by the Canadian Forest Service and represent germinant heights under a range of canopy density and site preparation conditions.

Overstory Canopy Closure (OCC): Overstory canopy closure is a restricted value (0 to 1) set by the user. Canopy closure is a function of disturbance history, stand structure, and composition. As used in this study, OCC is a measure of competitive influences based on the amount of shading by overstory trees and the resulting impact on the growth of germinants (Saunders and Puettmann 1999a and Chapter 2).

The value for OCC is calculated as 1- DIFN value. For a detailed explanation of DIFN, please refer to Chapter 2. DIFN values used in the development of the equation were obtained for individual trees from experimental plots used in the construction of the growth equations. DIFN values were obtained by using a LICOR LAI 2000 plant canopy analyzer (LICOR Industries, Lincoln NE). For information on the relationship between DIFN and basal area of overstory trees in various forest types, see Puettmann and D'Amato (in press).

Understory Competition (UC): Understory competition is a categorical variable (0 or 1) set by the user. This variable was developed to quantify the competitive influences of understory woody vegetation on the subsequent growth of white pine germinants. When the variable is set to 1 it represents understory (non-herbaceous) competitive influences on growth. The variable can be set to 0 to simulate complete understory vegetation control measures that result from silvicultural operations.

This variable was developed from the white pine database in the following manner. To isolate the influence of the overstory from the understory, DIFN values for 'open grown' trees were isolated and averaged by plot (mDIFN). Open grown trees are those where competing understory vegetation was repeatedly removed during the

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growing season. See Chapter 2 methods section for additional information. UC values were then calculated for control trees (no vegetation management) in each plot in the following manner: mDIFN – individual control tree DIFN. Negative values were corrected to 0 and the UC value for open grown trees was set to 0.

Herbaceous Cover (HB): Percent herbaceous cover is a continuous variable (0 to 100 %) set by the user. The value selected represents a visual estimate of the percent herbaceous ground cover in the immediate vicinity (1 m radius) of the seedlings. This variable characterizes the competitive influences of herbaceous plants within that radius of the germinant white pine. A complete description is located in the methods section of Chapter 2.

OCC X UC: This variable is included to recognize the influence the overstory canopy layer has on the abundance and growth of the woody shrub layer. The interaction is further discussed and illustrated in Chapter 2 (Figure 2.2). This value of the interaction within the specific growth equation is determined in the following equation.

[6]   OCC X UC value = OCC * UC * β_5 (interaction coefficient)

The value of the interaction β_5 coefficient varies by cover type (Table 3.4). When UC is set to 0 to reflect the absence of understory woody vegetation, the interaction value becomes 0.

End of Season Height (ESH): The end of season height is an output variable for this model. It represents the population height (cm) distribution for germinants at the end of the growing season.

Mortality sub-model (Figure 3.1c)

Second Year Germinants (SG): Input obtained from the output population distribution of the recruitment sub-model (GT). The population distribution of GT (mean ± sd) is used to represent surviving germinants from the first year that this sub-model modifies.

<u>Winter Mortality (WM):</u>   Set by the user to represent the range of mortality occurring in the winter following germination. Winter mortality is expressed as a proportion of the population removed. As with initial mortality (IM), this variable collectively summarizes the proportion of the germinant population subject to winter mortality as induced by a wide range of random elements such as: herbivory, mechanical damage; site factors such as frost heave; and physiological damage from desiccation or freezing. The influence of individual mortality agents is a function of random events, large and small scale weather patterns, stand/site history, disturbance patterns, stand structure, and local population dynamics. Determining causation for winter mortality is difficult in temperate forests due to the inability to observe what occurs under the snow pack. Winter mortality in germinants is highly variable which precludes making highly accurate estimates during an individual season. To parameterize this variable for the model application test, estimates for winter mortality were derived from Cornett *et al.* (1998).

<u>Spring Herbivory (SH):</u> Set by the user to represent the range of mortality that occurs due to browse by small mammals and deer. Spring herbivory is expressed as a proportion of the germinant population removed. As with the other mortality variables modeled, this variable collectively summarizes the proportion of the germinant population subject to mortality from a range of random herbivory sources. For germinants, it is assumed that herbivory equates to death due to limitations on the capacity for small seedlings to survive the removal of a large proportion of leaf area. Herbivory is a function of cover type, browse pressure due to animal population characteristics, and random elements such as snow pack levels and understory vegetation cover that affords hiding cover for white pine germinants.

The regional influence of herbivory on young white pine has been reported by Sauerman (1992), Saunders (1998), Saunders & Puettmann (1999a and 1999b), and Puettmann &Saunders (2001). The specific influence of herbivory on growth response documented in older seedlings is not used in this study due to the assumption of mortality. Saunders (1998) provides the best estimate for rates of browse on small white pine trees in northern Minnesota, with a reported incident rate of 32 % for seedlings < 30 cm tall. Overall, Saunders reports a mean browse rate of 38 % (range = 9-78 %) for all

seedlings, with terminal browse occurring on seedlings between 25 and 55 cm in height. Sauerman (1992) reports a browse damage rate of 48 % of trees in 69 % of surveyed white pine stands in northern Minnesota.

<u>Summer mortality (SM):</u>   Set by the user to represent the proportion of germinants removed due to a number of mortality agents in the second summer season. This mortality variable represents an estimate, which modifies the remaining germinant population distribution.

As with initial mortality (IM), this variable collectively summarizes the proportion of the germinant population subject to mortality induced by a range sources such as: climatic factors, desiccation, drought, heat injury, insect and small mammal predation, deer herbivory, disease, and mechanical damage. Sources used to establish the bounding properties for this variable include reports on white pine mortality by Smith (1940), Hocker (1961), Graber (1968), Cornett (1996), Cornett *et al.* (1998), Saunders (1998), the extensive white pine database generated by our Silviculture Lab Group (i.e. Two Harbors database from Chapter 2), and unpublished data from the Canadian Forest Service in Ontario (S. D'eon and B. Parker unpublished data). Smith (1940) reports a range of second year mortality for germinant white pine from 69 % to a high of 100%.

<u>Ending germinants (EG):</u>   An output variable representing the end of season germinant density.

Appendix 2

Cover Type Site Summary

Conifer cover type: The conifer cover type is based on the Cloquet Underplanting (CQ), which is part of a larger series of experiments designed to investigate the effects of the partial removal of a conifer overstory on the growth and survival of planted white pine. This experiment was established beneath a 100-year-old red pine stand. Part of the red pine overstory was thinned in 1996 to a residual density of 10-40 m^2/ha. The thinning created a residual range of overstory conditions across the site. In April-May 1996, approximately 650 3-0 white pine seedlings were planted in 21 plots located across the site. Growth and vigor were recorded through fall 2001.

Northern hardwoods cover type: The growth routine for the northern hardwoods cover type was developed from the Two Harbors site (TH), which is part of the white pine underplanting study. This 72-year-old stand is dominated by a paper birch and sugar maple overstory; the understory consists of large, dense patches of raspberry, blackberry, and beaked hazel. In the summer of 1994, a diameter-limited thinning operation was conducted across the site; this reduced basal areas to 5-20 m^2/ha. In April 1996, 867 3-0 white pine seedlings were planted in 24 plots of 36 seedlings (6 rows X 6 seedlings/row). The seedlings were planted under a variety of overstory density conditions. Growth and vigor were recorded through the fall of 2000.

Oak-maple hardwood cover type: The growth routine for the oak-maple-hardwood cover type is based on data from the Aitkin site (AK), which is part of a larger underplanting and physiology study. This site is predominately an uneven-aged northern hardwoods type, with much of overstory dominated by northern red oak and sugar maple. In spring 1995, several overstory and understory trees on the site have been girdled or thinned in order to create a range of overstory conditions, from very open to closed canopies. It was underplanted in 1996 with approximately 1200 3-0 white pine seedlings. Growth and vigor were recorded through fall 1999.